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Feeding and physiological energetics of the littoral Tellinoidea of Dublin Bay

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ABSTRACT

The littoral Tellinoids, marine bivalve clams, are an important component of the Dublin Bay ecosystem, comprising a third of benthic macrofaunal biomass and providing a key conduit in the flow of energy through the system. UNESCO Dublin Bay Biosphere is a site of high ecological value. The purpose of this investigation is to examine the feeding mode and physiological energetics of the littoral Tellinoidea (Blainville, 1814) of Dublin Bay, in order to better understand resource partitioning and niche division within this superfamily. The superfamily of the Tellinoidea all share a similar body plan. The five species of Tellinoids examined were *Scrobicularia plana, Macomangulus tenuis, Limecola balthica, Fabulina fabula* and *Donax vittatus*. Suspensivores and deposivores have distinct roles in nutrient cycles and partition resources differently. Suspension feeders link benthic and pelagic systems and compete for the same resources, while deposit feeders recycle nutrients and partition resources. Distribution, abundance and biomass of all macrobenthos was recorded in the field. For the first time, palp to gill area was employed to determine the feeding mode of five members of this superfamily. Diet composition and suspended particle capture efficiencies were established. Feeding variables, Scope for Growth (SFG) and Gut Passage Time (GPT) were determined. It was found that the Tellinoidea comprise 32% of benthic biomass of the areas investigated. There were two distinct environmental biotopes in the Dublin Bay littoral zone area examined, distinguished by silt, redox potential discontinuity (RPD), salinity and biota. *M. tenuis* was the most widespread Tellinoid, and the only species found in both environments. The type of feeding undertaken by bivalves, deposit or suspension, defines their impact on the system. *D. vittatus* and *M. tenuis* were classified as suspensivores, *L. balthica* was classified as deposivorous, and *F. fabula* and *S. plana* as using both feeding modes. Palp:gill area ratios of *L. balthica* were highest, and significantly higher than those of *S. plana*. *M. tenuis* and *F. fabula's* differences in palp:gill area ratios were confirmed using a novel photographic analysis technique developed. Picoplankton < 2 μm formed a large part of the diet of the Tellinoids examined, especially for *D. vittatus*. Foraminifera were recorded in the diet of *L. balthica,* a first record. Spheroidal plankton constituted approximately half the diet of the Tellinoid species examined, more in *D. vittatus*, and less in *M. tenuis*. Particles > 4 μm were more efficiently captured from a suspension of multiple particle sizes, and no distinctive peaks in capture efficiency were noted. The Tellinoid species tested here did not partition niches according to particle sizes captured. SFG and GPT highlighted energetic efficiency differences, with *D. vittatus* exhibiting negative SFG under the test conditions. *M. tenuis*, the most abundant and widespread Tellinoid, showed the greatest potential in terms of competitive ability, while *D. vittatus* showed the least. *L. balthica* and *S. plana* are found in the same environments, sharing a similar feeding mode and capturing plankton (prey) size ranges in experimental conditions with similar efficiency, but with *S. plana* ingesting smaller particles (< 2 μm) in its diet. *F. fabula* and *D. vittatus* were also found in similar environments to each other, mostly near the Low Water Mark in clean sand, and both were subject to potential increasing competition with *M. tenuis* towards the mid-shore. *M. tenuis* is found in all environments, it has high SFG, and is much more abundant where *F. fabula* and *D. vittatus* also occur. The outcomes of the work, elucidating feeding mode and feeding energetics of Tellinoids, can be applied to future network analyses of Dublin Bay's ecosystem, providing a basis for evidence-based conservation objectives.

Declaration

I, the undersigned, declare that this work has not previously been submitted to this or any other University, and that unless otherwise stated, it is entirely my own work.

Linda Daniels

Dated: March 31, 2018

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Summary

Suspensivores and deposivores are important members of estuarine ecosystems, recycling pelagic and benthic nutrients respectively. Suspension feeders link benthic and pelagic systems and compete for the same resources, while deposit feeders recycle nutrients and partition resources. Differentiating between these groups gives a better understanding of nutrient cycling pathways and trophic transfers in marine systems. This work focuses on the superfamily of the Tellinoidea (Blainville, 1814), which all share a similar body plan. The five species of Tellinoids examined were *Scrobicularia plana, Macomangulus tenuis, Limecola balthica, Fabulina fabula* and *Donax vittatus*. These species are an important component of the ecosystem of UNESCO Dublin Bay Biosphere, a site of high ecological value. Tellinoids comprise a third of benthic macrofaunal biomass at this location and provide a key conduit in the flow of energy through the system.

Tellinoids were sampled using cores along 5 transects, at three locations in Dublin Bay and another at Gormanstown Beach, Balbriggan. Tellinoids accounted for 32% of all macrofaunal biomass. Individual Tellinoid species were associated with distinct biotopes: *M. tenuis* was found at most stations and especially abundant in cleaner, sandy areas; *L. balthica* and *S. plana* in muddy sand; *D. vittatus* and *F. fabula* were found separately in clean sandy habitats around low water.

The type of feeding undertaken by bivalves, deposit or suspension, defines their role in the system. The palp area to gill area ratio (P:G) is indicative of a feeding mode where a high ratio signifies deposit feeding and a low ratio indicates suspensivory. The gills and palps of five species of Tellinoids were examined together for the first time, using the P:G area ratio to classify their mode of feeding. The average P:G ratios found were as follows: *L. balthica*: 4.12; *S. plana*: 1.38, *F. fabula*: 1.31, *M. tenuis* : 0.78, *D. vittatus*: 0.5. A larger than expected difference between P:G area ratio of *L. balthica* and *S. plana* was found. After examination of allometric growth of palps and gills relative to dry flesh weight and length to determine whether feeding mode changes with growth, no conclusive differences were identified.

The comparative dietary composition of the Tellinoids in their natural habitats was determined by examination of the plankton shapes and sizes present on their crystalline styles. In all species except *S. plana*, $> 65\%$ of the energy content was provided by spherical and rectangular morphospecies. The crystalline styles of *D. vittatus* were dominated by picoplankton (<2 μm); by contrast picoplankton were a minor constituent of *L. balthica*s diet. It was not expected that plankton <4 μm would form a substantial part of the diet of Tellinoids as they

are commonly thought to eat particle over 4 μm. Foraminifera were found on the crystalline style of *L. balthica*, a previously undocumented occurrence.

Particle size preference is used to determine what, if any, size of particles were preferentially captured from suspension (i.e. captured in greater than environmental proportions). The results indicate that large sized particles in suspension were captured more efficiently than small particles by all Tellinoid species. *F. fabula* captured a greater proportion of particles from larger size categories than particles in smaller size categories from the available stock suspension. *M. tenuis* exhibited a much weaker linear relationship between size and capture efficiency than *F. fabula*. *D. vittatus*, *S. plana* and *L. balthica* all captured larger particles more efficiently than smaller particles, but the relationship was not linear, with particles over a threshold (≈4.2 μm) being captured with approximately equal efficiency, as opposed to the continued increase in efficiency with size seen in *F. fabula* and *M. tenuis*.

Scope for growth (SFG), chlorophyll analysis and Gut Passage Time (GPT) were examined, in order to categorise the energetic niche. *F. fabula* had the highest SFG and *D. vittatus* displayed a slight negative SFG, the results are consistent with ranges of SFG in spring reported by previous studies. The SFG methodology has not been applied to numerous members of the Tellinoidea in tandem before, and is a useful way of making direct energetic comparisons. GPT varied by species with *D. vittatus* having the shortest GPT and *S. plana* having the longest. Chlorophyll values analysed between faeces from the natural diet compared with faeces produced from a diet of pure *Isochrysis galbana* a flagellate, were inconclusive.

Strong correlations were seen between P:G area ratio and silt content, consistent with deposit feeders normally being found in high silt environments. P:G also correlated positively with size of particles in the natural diet found on the crystalline style, perhaps indicating that deposit feeders ingest larger particles. *M. tenuis*, the most abundant and widespread Tellinoid, displayed the greatest potential in terms of competitive ability, while *D. vittatus* showed the least. *L. balthica* and *S. plana* may compete for shared resources, being found in the same environments, sharing a feeding mode and capturing *I. galbana* size ranges with similar efficiency, but with *S. plana* ingesting smaller particles in its natural diet. *F. fabula* and *D. vittatus* were also found in similar environments to each other, mostly near the Low Water Mark in clean sand, consuming small particles in the natural environment, but capturing larger particles more efficiently, and both being subject to increasing competition with *M. tenuis* towards the mid-shore. *M. tenuis* is found in all environments, has high SFG, and is much more abundant where *F. fabula* and *D. vittatus* also occur. The outcomes of the work, elucidating feeding mode and feeding energetics of Tellinoids, can be applied to future network analyses of Dublin Bays ecosystem, providing a basis for evidence-based conservation objectives.

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Chapter 1

Introduction

In understanding environments, in which bivalves play an important role, it is necessary to understand the factors which influence the nature and rate of bivalve feeding. Suspensivores and deposivores have distinct roles in nutrient cycles. Suspension feeders link benthic and pelagic systems, while deposit feeders recycle nutrients. Marine deposivores that consume detritus that collects on the substratum at the water sediment interface, tend to partition resources to reduce competition, whereas suspensivores that consume suspended matter and food particles from seawater, compete for a common size range of particles (Levinton, 1972).

Suspensivores are subject to unpredictable and fluctuating food supply, as they filter what is available in the water column, which changes with hydrological, cyclical (e.g. flood/ebb, neap/spring) and seasonal variation. Suspensivores are predicted to have a less stable trophic structure than deposit feeders, where one species may completely exclude others by competition for feeding space. Deposivores depend on a predictable and stable food supply, and are more likely to be specialist feeders. Specialised feeding behaviour, predicted for deposivores, such as the strong preference of a species for a very specific size or type of algae, is thought to have emerged owing to competitive interaction between deposit feeding bivalves (Levinton, 1972).

1.1 Levinton's hypothesis (1972)

Energy acquisition efficiency and competition for resources are Darwinian drivers of evolution. The pathway from food to expendable energy within an organism is complex and involves sensing, capture, sorting, ingestion, digestion and assimilation. Food is a limiting factor in deposit feeding communities but not to the same extent in suspension feeding communities

(Olafsson, 1986) where food is less limited in suspension. This limitation is one of the drivers of different levels of specialisation in Levinton's (1972) hypothesis, which, if true, has the following consequences:

- Niche width, in terms of particle size, is broad for suspensivores and narrow for deposivores.
- Food selectivity is high for deposivores and low for suspensivores.
- A small number of species account for the majority of the biomass in suspensivore communities (high dominance), whereas low dominance is exhibited in deposivore communities.

Energy flow through macrofauna is an important link between primary producers and secondary consumers in marine ecosystems. Determining the component energy provides descriptive information about individual system functioning. The structure of deposivore communities is more diverse and resistant to change than that of suspensivore communities (Levinton, 1972), and is evident in many marine communities (e.g. horse mussels *Modiolus*, abra clams *Abra*, venus clams *Venus* and brittle stars *Amphiura*; Warwick,1982). Energy flow within an organism is determined by its feeding mechanism, capture efficiency, energy conversion and respiration.

Suspensivore assemblage is vulnerable to any problems with dominant species, particularly in communities with high annual turnover (Warwick, 1982; Levinton, 1972). In such communities, failure to recruit, or high mortality of the dominant species, would have a much greater effect than the failure of one important deposivore species in a community where production is more equitably distributed, and where other species would buffer the change (Warwick, 1982). Typical assemblages results in one, or very few, species dominating the production of biomass in predominately suspension feeding communities, whereas in deposit feeders, production is distributed more equitably among species (Warwick, 1982). Suspensivorous species are also inherently more vulnerable to catastrophic events, such as disruption in supply of phytoplankton (Sheehan and Hansen, 1986; Rhodes and Thayer, 1991).

A consensus is yet to be reached on the nature of bivalve feeding and how the selection of particles occurs (Rosa *et al.*, 2013). Contrary to the view that feeding in bivalves is an "automatised" process (i.e. feeding is independent to the other processes in a bivalve) (Jorgensen, 1996), the process is generally considered to be a complex synergy between behavioural, physiological and morphological traits which respond to variations in available

food (Bayne, 1998). The Tellinoids exhibit a range of feeding behaviours, from suspensivore to deposivore (Yonge, 1949), which can make it difficult to meaningfully relate assemblage indices, namely diversity and dominance, for the superfamily (the Tellinoidea) to feeding type, as this would typically require feeding type to be a fixed parameter. One commonly accepted example of variability in feeding type is the Tellinoid *L. balthica*, which is both a suspension and a deposit feeder (Yonge, 1949).

Recent approaches to non binary classification of functional trait includes the assignment of a fuzzy code for each trait reflecting the degree to which the species in that assemblage conforms to or expresses that trait (Bremner *et al.*, 2003). The classification in Bremner *et al.* (2003) rated organisms as scavengers and predators, in addition to deposivory and suspensivory. As the Tellinoidea do not exhibit scavenging or predatory behaviours, their classification can be expressed as their relative degree of deposivory or suspensivory. Stable isotope analysis (SIA) is another method for determining the trophic ecology of bivalves. SIA works on a longer time-scale to gut content analysis, measuring material assimilated over the previous two – six months as opposed to hours for gut contents (Maloy *et al.*, 2013). *Mytilus* sp. were found to have isotopic signatures reflecting a trophic level difference of up to 0.8 between individuals or up to 0.5 between populations, a large degree of trophic plasticity. The gut contents analysis found that the ingested material differed from that in the water column, indicating some degree of selection (Maloy *et al.*, 2013).

1.2 The Tellinoidea

Previously referred to as Tellinacea (Blainville, 1814), the Tellinoidea (Veneridae, Heterodonta) are comprised of a dynamic and diverse superfamily of bivalves (Prezant, 1998) that are commonly found in muddy or sandy benthic communities (Kawai *et al.*, 1993). The Tellinoidea are a very successful superfamily of lamellibranchs, as is apparent from their vast abundance in soft, deposit laden strata, in both littoral and sublittoral zones (Yonge, 1949). Tellinoids are usually found in temperate areas and are common around the coasts of Britain and Ireland (Vaught *et al.*, 1989). Dublin Bay is host to communities of five littoral species: *Donax vittatus* (da Costa 1778), *Scrobicularia plana* (de Costa 1778), *Limecola balthica* (Linnaeus 1758), *Macomangulus tenuis* (da Costa 1778) and *Fabulina fabula* (Gmelin 1791), which differ in physical appearance as well as in feeding behaviour (Figure 1.1). Where Tellinoids are found, they are commonly the dominant species in the ecosystem. *F. fabula* for example, has been found to occupy 28% of the biomass of an infaunal community in Heligoland

(Salzwedel, 1979) and *L. balthica* accounted for 50% of the total macrofaunal production in the Cumberland basin (Cranford *et al.*, 2005).

The Tellinoidea are comprised of 180 extant species which have adapted to almost every marine environment (Yonge, 1949; Laudien *et al.*, 2003; Yu *et al.*, 2015), including some freshwater species. The different species are easily identified using morphological and ecological characteristics, with an established morphological taxonomic system in place (Bieler *et al.*, 2010; Coan and Valentich-Scott, 2012). Within the superfamily there are various species with commercial and ecological value (Yu *et al.*, 2015), notably: *Moerella iridescens* (edible), *Sinonovacula constricta* (edible, aquaculture in China and Japan), *D. vittatus* (edible) and *L. balthica* (biological indicator). *L. balthica* 's burrowing behaviour is a potential mechanism for ecosystem change prediction (Compton *et al.*, 2016). Tellinoids form an important component of the marine food web (Trevallion, 1971) and are an ideal subject for testing feeding niche differentiation and feeding mode, as the superfamily is comprised of both deposit feeders and suspension feeders.

1.2.1 Nomenclature

The accepted names of three of the species have changed recently (Huber *et al.*, 2015). These are *Tellina tenuis*, which has been renamed as *Macomangulus tenuis*; *Tellina fabula*, which has been renamed as *Fabulina fabula*; and *Macoma balthica*, which has been renamed as *Limecola balthica*. The species are referred to throughout this thesis by their currently accepted names and classifications (Figure 1.2). Previous and current cladograms, containing the five species of interest, indicate that no change in the comparative degrees of relatedness has occurred owing to reclassification, with *F. fabula* and *M. tenuis* moving to two separate genera, but remaining more closely related to one another than to any other Tellinoid species (Figures 1.3, 1.4).

1.2.2 Evolution

The earliest heterodonts, the Astartacea, were the ancestors of the Tellinoidea, with paleontological evidence suggesting that the earliest animals were suspension feeders. Early Tellinoids lived vertically within burrows in shifting sand, in a similar fashion to the current members of the Donacidae. Selective feeders subsequently emerged, with the acquisition of deposit feeding, and its attendant morphology, being the final stage in the Tellinoidean evolution (Pohlo, 1982; Wade, 1965). *D. vittatus* occupies the same niche as its original heterodont

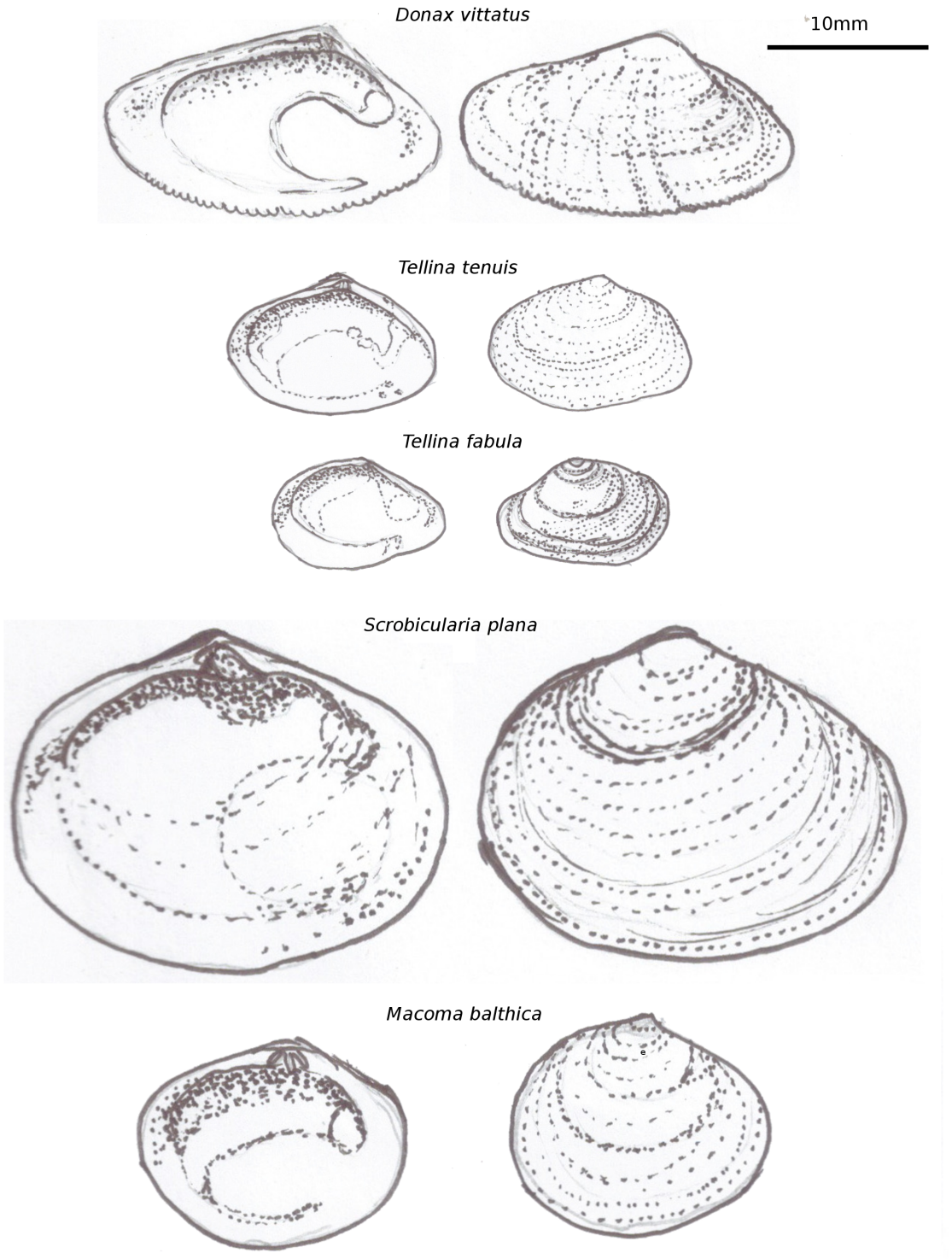

Figure 1.1. The relative size, by species, of Tellinoids sampled from Dublin Bay. All diagrams represent the average size of a mature adult.

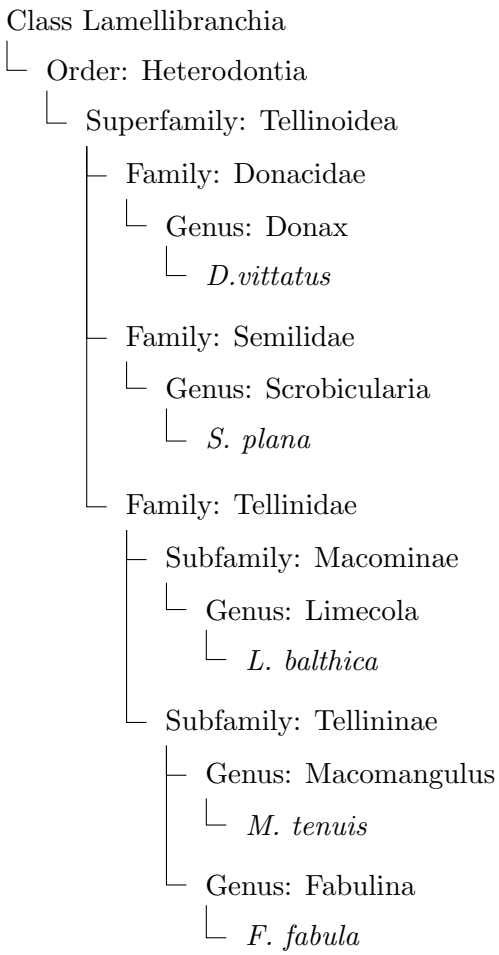

Figure 1.2. Taxonomic Classification of the Superfamily Tellinoidea and the family association of the species. (From WoRMS and Huber *et al.* (2015), with phylogeny based on Combosch *et al.* (2017)).

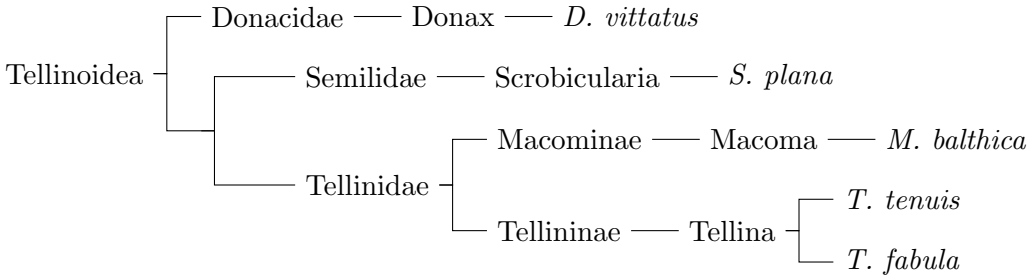

Figure 1.3. Cladogram of the Tellinoids examined (phylogeny based on Combosch *et al.* (2017)).

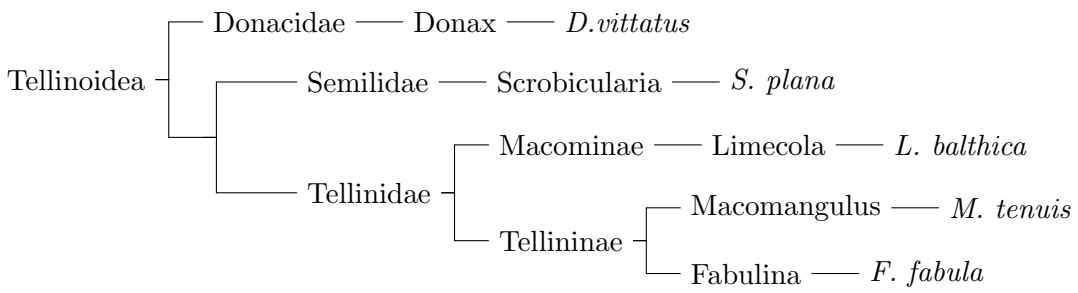

Figure 1.4. Cladogram of the Tellinoids examined based on the revised classification (From WoRMS and Huber *et al.* (2015), with phylogeny based on Combosch *et al.* (2017)).

ancestors, whereas other Tellinoids such as *L. balthica* , *S. plana* , *F. fabula* and *M. tenuis* are more specialised and have evolved to occupy different niches.

The Tellinoideans are lamellibranchs (class lamellibranchia; platelike gills), which includes the subclasses: filibranchia, pseudolamellibranchia and eulamellibranchia. The Tellinoids possess a eulamellibranch gill structure, together with the majority of bivalves, with homorhabdic lamellae (Ridewood, 1903) and lateral frontal cilia (Atkins, 1937). Most eulamellibranchs suspension feed, with deposit feeding noted only in the Tellinoidea and Luninacea (Yonge and Thompson, 1976; Morse and Zardus, 1997; Stead *et al.*, 2002). Deposit feeding and facultative deposit feeding Tellinoids have evolved long siphons to explore the sediment surface and larger labial palps to sort ingested material, while obligate suspensivores retained short siphons that lie flush with the marine sediment and large gills that serve as the main food collector and processor.

The Tellinoidea are a well defined superfamily with distinguishing features, which include very long, narrow, mobile and separated siphons, formed by the exclusive fusion of the inner mantle lobes (Thiele, 1935; Stanley, 1970; Vitonis *et al.*, 2012; Yonge, 1948, 1949). Considerable genetic work has been conducted on the Tellinoidea owing to their commercial importance (Yu *et al.*, 2015; Combosch *et al.*, 2017; Yuan *et al.*, 2012; Ponder and Lindberg, 2008). These investigations confirm the placement of the families: Donacidae, Tellinidae and Semelidae within this superfamily.

1.2.3 Feeding process

As part of the feeding process in all bivalves, a current is generated and water containing food particles flows through the filaments over the gill faces. The particles get trapped in the gills' closely aligned filaments. Cilia move the particles via ventral food grooves located at the

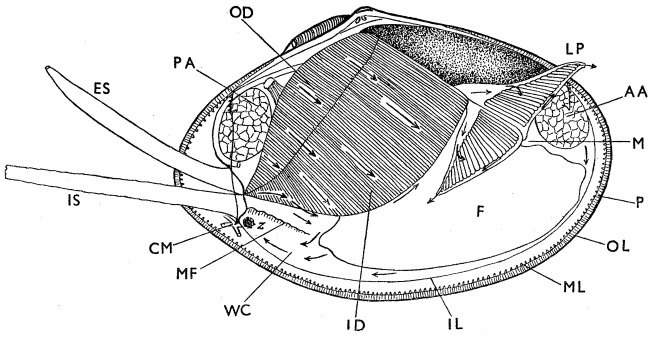

Figure 1.5. *M. tenuis*, viewed from right side after removal of right shell valve and mantle lobe (magn.x5). AA, anterior adductor; CM cruciform muscle; ES, exhalant siphon; F, foot ID, inner demibranch; IL, inner lobe of mantle edge; IS, inhalant siphon; LP, labial palp; M, position of mouth (in mid-line); MF, mantle fold; ML, middle lobe of mantle edge; OD, outer demibranch; OL, outer lobe of mantle edge; P, periostracum covering region between outer mantle lobe and periostracal groove; PA, posterior adductor; WC, waste canal; z, accumulation of pseudofaeces. Arrows indicate direction of ciliary currents. Image credited to Yonge (1949)

bottom of each demibranch to paired palps located on either side of the mouth. The palps sort the particles according to both size and nutritional value (Figure 1.5)(Ward *et al.*, 2000; Gosling, 2008). Gills and palps are actively involved in the particle selection process in the Tellinoidea (Morton, 1983). Suspensivores possess smaller palps compared to deposivores, as they inhale fewer sedimentary particles, and receive food particles that may already have been sorted by the gills (Stead *et al.*, 2002)

In some species, the inhalent siphon which reaches a length of four to five times that of the shell (Yonge, 1949), can move independently of the exhalent siphon, and is used to collect material from the underlying substratum. The lateral cilia of the gills (ctenidia) produce a strong inhalent current that causes material beneath or just above the sediment surface to be sucked into the pallial cavity and onto the frontal surfaces of the gills (Yonge, 1949; Hughes, 1969; Levinton *et al.*, 1996). Capture of deposit material by the gills is functionally similar to the removal of suspended material from the water columns, and the gills have special adaptations to handle large masses of material (Atkins, 1937; Stasek, 1961).

Tellinoids can feed on a broad spectrum of prey items, from bacteria to zooplankton, and in some species, diet may change if an alternative food is presented (Gili *et al.*, 2001; Arruda *et al.*, 2003). This type of trophic plasticity, consuming a broad range of food sources, is

characteristic of suspension feeders (Ribes *et al.*, 1999). Trophic plasticity allows organisms to better cope with fluctuations in the availability, seasonality and delivery of different resources in the water column, which provides a fitness advantage over other species (Gili *et al.*, 2001).

Suspensivores have been observed to occupy clean sandy substrates, while deposivores are typically found in muddy sediment (Yonge, 1949). As a result, suspensivores spend a greater amount of energy in pumping water than deposivores. The type of feeding undertaken by bivalves defines their impact on the system in which they live. Early work on morphometrics and feeding mode concluded that palps were correlated with the degree of deposit-feeding in the Tellinoidea (Yonge, 1949) and Veneracea (Ansell, 1961). All the Tellinoidean species were originally classified as deposivores on the basis of their separate, mobile, extensible siphons (Atkins, 1937; Yonge, 1949). Recent work has resulted in a reclassification of genera (Huber *et al.*, 2015). Suspensivores have less need for extensible siphons, as they filter the water column indiscriminately. The siphons of *D. vittatus* are shorter than those of, for example, the Tellinidae or *S. plana* (Figure 1.6). Within any bivalve species, the relative areas of the gills and palps can be related to changes in local food conditions, demonstrating a degree of phenotypic plasticity (Compton *et al.*, 2008).

1.2.4 Feeding behaviours and ecology

The five species of Tellinoids living in Dublin Bay can be classified on a scale from deposit to suspension feeding, in order of increasing tendency to suspension feed, as follows: *S. plana*, *L. balthica*, *F. fabula*, *M. tenuis*, *D. vittatus*. Morphological configurations suggest the variety of feeding modes, including assumed exclusive suspension feeding in the Donacidae, and deposit and facultative deposit feeding in the Tellinidae and Semelidae (Yonge, 1949; Pohlo, 1969, 1982; Domaneschi, 1995). These families all use suspension feeding, however, when conditions are appropriate (Olafsson, 1986; Lin and Hines, 1994). Bivalves can also respond to changes in environmental conditions by altering feeding modes (Bayne, 1998).

Most of these five species cannot be exclusively assigned to one mode of feeding. Feeding behaviours can also change with age and season (Salzwedel, 1979; Strohmeier *et al.*, 2012), so experiments must ideally be carried out on all species at the same time of year or at several times during the year. The distinction between deposivore and suspensivore lamellibranchs may be largely artificial, as most Tellinoids can vary their mode of feeding according to environmental conditions (Ward and Shumway, 2004). Tellinoids are the only bivalves that engage in a type of deposit feeding known as surface siphon feeding (Levinton, 1982). Surface

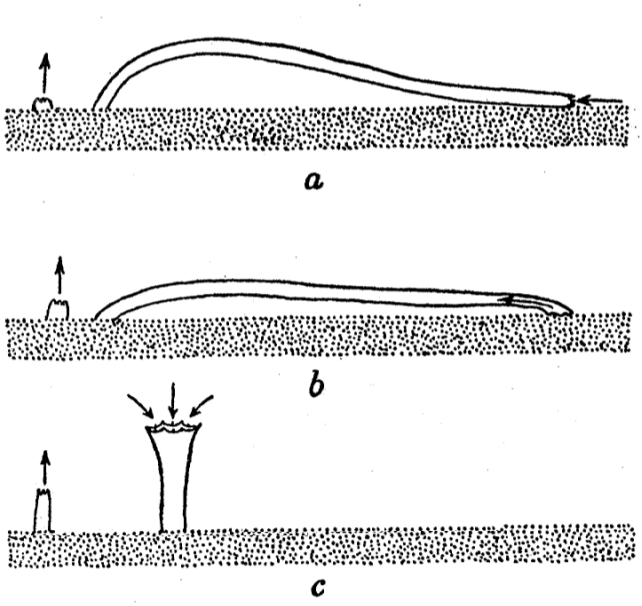

Figure 1.6. Appearance of siphons above substratum in a: *Fabulina sp.*, *Macomangulus sp.* and *Limecola sp.*; b: *Scrobicularia sp.*; c: *Donax sp.* with arrows showing the direction of water flow (not to scale.) Adapted from (Yonge, 1949)

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siphon feeding, drawing in material from the sediment water interface, is however not common to all species in the superfamily as once proposed (Yonge, 1949). Species with protective tubercles around their inhalent siphon are generally suspension feeders, with these tubercles acting to keep out sediment particles (Levinton, 1982). The Tellinoids of Dublin Bay settle and mature at different sizes and exhibit differing feeding behaviours (Table 1.1).

Table 1.1. Maximum shell length, settlement shell length and shell length at reproductive maturity of five species of Tellinoid bivalves from Dublin Bay.

Species	Shell Length (mm)			References
	Max	Settlement	Maturity	
D. vittatus	40	0.25-0.35	10	Degraer *et al.* (2006), Webb (1986), Cardoso and Veloso (2003)
M. tenuis	19	0.25-0.3	10	Oliver *et al.* (2010b), Gosling (2008), Wilson (1997)
F. fabula	20	0.25-0.28	10	Oliver *et al.* (2010a), Webb (1986), Wilson (1997), Salzwedel (1979)
S. plana	63	0.25-0.3	20	Fish and Fish (1996), Raleigh and Keegan (2006), Frenkiel and Mouëza (1979)
L. balthica	25	0.2-0.3	10	Gilbert (1973), Jorgensen (1996), Honkoop *et al.* (1998)

L. balthica primarily deposit-feeds both actively and passively (Yonge, 1949; Reid and Reid, 1969; Warwick and Price, 1975; Levinton, 1982; Hummel, 1985), but is also known to suspension-feed (Ratcliffe *et al.*, 1981; Kamermans, 1994; Olafsson, 1986). *L. balthica* is commonly found in muddy sand (Holtmann *et al.*, 1996), gravel (Atkins, 1937), and often in deoxygenated sand in shallow neritic waters (Stephen, 1929; Yonge, 1949). It is likely that *L. balthica* 's behaviour switches between feeding modes based on the velocity of the surrounding water, with high-velocity leading to suspension feeding and low velocity to deposit feeding. The type of feeding is linked to the sediment in which it is found; in muddy substrata *L. balthica* tend to deposit feed (Brafield and Newell, 1961; Olafsson, 1986, 1988), while suspension feeding in sandy areas (Bubnova, 1972; de Goeij and Honkoop, 2002; Navarro *et al.*, 2008), however, their feeding mode can change within an hour in response to varying conditions (Olafsson, 1986). *L. balthica* will suspension feed after siphon cropping if not in the presence of another suspension feeder (Skilleter and Peterson, 1994). In an examination of suspensivore and deposivore stomach contents in the Wadden Sea, Netherlands, while algal content in the stomachs of most species varied with the tidal cycle, *L. balthica* differed, with algae present in its stomach throughout (Kamermans and Huitema, 1994). This indicates its ability to draw water and algae from the sediment when the tide is out.

S. plana is primarily classified as a deposivore (Yonge, 1949; Hughes, 1969, 1971; War-

wick and Price, 1975; Levinton, 1982; Sola, 1997). Similar to *L. balthica* , however, *S. plana* also ingests algae from the water column (Kamermans, 1994; Hughes, 1969) and has also been classified as a facultative suspension feeder (Orvain, 2005). *S. plana* is typically found in soft substrata, rich in organic debris, such as intertidal mud flats (Hughes, 1970b), stiff mud (Atkins, 1937) or where there is some dilution with fresh water. *S. plana* can live high on the shore and in very brackish waters, giving it a competitive advantage in some environments (Yonge, 1949).

F. fabula has been classified as both a selective deposit and suspension-feeder (Muus, 1973; Withers, 1977; Warwick *et al.*, 1978; Salzwedel, 1979; Wilson, 1990; López-Jamar *et al.*, 1995). *T. fabula*, however, is solely a suspension-feeder up until the age of one and a half years, after which it changes between feeding methods according to environmental conditions, indicating a shift of strategy with age/size (Salzwedel, 1979). *T. fabula* is typically located in fine clean silty sand (Atkins, 1937; Holtmann *et al.*, 1996).

M. tenuis is a suspension-feeder with a tendency to selective deposit-feeding (Trevallion, 1971), indicated by its gut containing a bacteriolytic enzyme (lysozyme) for deposit feeding digestion (McHenery *et al.*, 1983). The species maintain feeding territories through inhalent siphon contact while deposit-feeding (Holme, 1950), although the establishment and maintenance of such territories may be a localised phenomenon as this behaviour and resultant distributions have not been observed elsewhere. Wilson (1976b) did not observe this same spatial distribution pattern in populations in Kames Bay, Scotland, but rather a distribution suggestive more of suspension-feeding, although it was acknowledged that opportunistic feeding occurs. *M. tenuis* is commonly found in clean intertidal sand (Atkins, 1937; Trevallion, 1971).

D. vittatus are obligate suspensivores with short and wide siphons (Yonge, 1949; Pohlo, 1969; Levinton, 1991). *D. vittatus* is typically found in clean fine sand (Holtmann *et al.*, 1996) or very firm sand sometimes displacing *M. tenuis* (Stephen, 1929; Yonge, 1949) and silty sand or shell gravel (Atkins, 1937). It is specialised for life in firm sand practically devoid of organic matter (Yonge, 1949) and is rarely found in substrata with high organic content.

1.2.5 Feeding selectivity

Although organic material which is available to bivalves is mixed with silt, bivalves are able to preferentially select nutritive particles such as algae and reject particles of poor nutritive

value as pseudofaeces (Hawkins *et al.*, 1996, 1998). Bivalves are also capable of discriminating between similar sized algal cells (Shumway *et al.*, 1985). The ability to distinguish between different food types could be a means whereby coexisting and potentially competing species partition available food resource (Shumway, 1990). Bivalves can actively reject specific particles rather than processing automatically. Video endoscopy has overturned the perception of bivalves as bulk processors of particulates (Baker *et al.*, 2000; Ward *et al.*, 1998, 1993). Retention efficiency of species with eulatero-frontal ciliary tracts has been found to be much greater for particles below 7 μm (Mathers, 1974), indicating that evolved particle size preferences do exist. The amount of food ingested, rather than particle concentration, controls the rejection rate of excess material in large deposivores (Winter, 1969, 1978). It is, however, unclear if this is true in all deposivores.

1.2.6 Position in ecosystem food webs

The Tellinoidea occupy the primary consumer/secondary producer trophic level. Their sources of food include detritus and bacteria as well as algae and other phytoplankton, giving them an important role as recyclers in shallow water marine, estuarine and intertidal ecosystems. The consumption and loss to predation of Tellinoids does not fully capture their importance in food webs. Tellinoid siphons, particularly longer siphons of deposit feeders, are exposed and vulnerable to predation/cropping and provide an important food source for juvenile flatfish (Trevallion, 1971; Gilbert and Suchow, 1977; De Vlas, 1979; Lockwood, 1980; Poxton *et al.*, 1983; Pekkarinen, 1984; De Vlas, 1985; Zwarts, 1986; Bonsdorff *et al.*, 1995), crabs (Hughes, 1969; Kamermans and Huitema, 1994) and birds (Ansell, 1981; McLachlan *et al.*, 1996). Regeneration of cropped siphons occurs and has been described for *M. tenuis* (Trevallion, 1971), *S. plana* (Hodgson, 1982), *L. balthica* (Pekkarinen, 1984) and *D. vittatus* (Ansell *et al.*, 1999). There is a high bird predator density and juvenile fish population in Dublin Bay, especially at Bull Island, making siphon cropping likely (Wilson and Parkes, 1998). Siphon cropping by fish and crabs forms part of a complex interaction, which makes the bivalves more accessible to predation by waders, such as oystercatchers *Haematopus* (Hughes, 1970b). The bivalve's burrowing depth is somewhat limited by its siphon length, and with a short siphon it must stay close to the sediment surface in order to feed, bringing it within the range of a bird's beak. Foot nipping by fish is also common (Salas *et al.*, 2001) and *L. balthica* are an important prey item for knot (*Calidris canutus*) as are its annual spat-fall (the settling of young larval bivalves to the substratum) (Zwarts and Blomert, 1992). Besides the

general role that bivalves play in the recycling of nutrients, their biodeposition is particularly important in introducing accessible nutrients to the rhizosphere where submerged aquatic plants, such as *Zostera noltii* can utilise them (Peterson and Heck, 1999). The grazing of particulates also reduces turbidity which increases light availability to the sea bottom which can enhance the growth of anchored plants such as seagrass (Newell and Ott 1999 in Ward and Shumway 2004).

Tellinoids act as bioturbators and ecosystem engineers, a concept introduced by Jones *et al.* (1994), modifying their physical habitat and providing an ecosystem service in the areas in which they live. The impact of bivalves as ecosystem engineers also includes the provision of shell material (Gutiérrez *et al.*, 2003). All of the Dublin Bay littoral Tellinoids which appear on the bioturbator classification of Queirós *et al.* (2013) are surficial modifiers, which have a limited regenerative impact on the sediment. They are all identically classified in their movement and bioturbation indices at 2/4 and 2/5 respectively (Queirós *et al.*, 2013).

1.2.7 Distribution

The Tellinoidea have a global distribution from the intertidal to the shallow waters of the continental shelf, and throughout Irish coastal waters. Most bivalves show a preference for a particular substratum (Gosling, 2008). Within its preferred substratum *L. balthica* frequently moves horizontally while *S. plana*, despite possessing the ability to do likewise, very seldomly moves horizontally, and has been found with touching shells and siphon-siphon interaction that does not affect feeding behaviour. While *M. tenuis* has a slight tendency towards occurring in high densities, it otherwise disperses randomly, suggesting a preference for suspension feeding. Spatial distance in *M. tenuis* in high densities has been hypothesised to be limited by siphon interaction while deposit feeding (Holme, 1950), although this work was later contradicted (Wilson, 1976b).

1.2.7.1 Factors affecting distribution

The habitats that can be colonised by Tellinoids vary considerably. Deposivores need a soft type of sediment to probe with their siphons, while suspension feeders often live in coarser, sandy material (Diaz and Rosenberg, 1995; Gaston *et al.*, 1998; Rakocinski *et al.*, 2000). Tidal height is another major factor, with *F. fabula* and *D. vittatus* generally found in the sublittoral and low littoral, *M. tenuis* extending from the littoral into the sublittoral, and *L. balthica* and *S. plana* being found in greatest numbers in the littoral, mid-tidal zone.

Other factors affecting suitability for colonisation include geographical location, salinity and perturbation (Anderson, 1972; Wilson and Elkaim, 1991).

1.2.8 Spatial structure of populations and population dynamics

Suspensivores generally do not establish feeding territories, and, therefore, only experience indirect competition effects, such as competition for space in the case of high infaunal densities (Holme, 1950; Wilson, 1976a) or resource depletion in large epifaunal banks (Okamura, 1986). Conversely deposit feeders maintain and defend territories (Holme, 1950) and, therefore, experience direct competitive interaction, although Wilson (1977) did not find supporting evidence for *M. tenuis* defending territories and concluded that the species was not deposivorous. The spatial distribution of *S. plana* has been found to be random in nature in areas of uniform physical conditions (Hughes, 1970b), indicating territories are not being maintained. Certain characteristics of Tellinoid populations, such as stability, can be inferred from their feeding type. In Northern European estuaries, severe winters result in high densities of intertidal bivalve recruits with the reverse being true in mild winters (Philippart *et al.*, 2003). Population dynamics are strongly related to sea temperatures. Rising temperatures have been seen to affect recruitment by decreasing reproductive output and by springward advancement of spawning, which is owing to the decoupling of spawning time and phytoplankton bloom (Philippart *et al.*, 2003).

1.2.9 Reproduction and life span

The Tellinoidea partake in broadcast spawning and fertilisation happens when gametes released by the separate sexes meet in the water column (Luttikhuizen *et al.*, 2011). Tellinoids begin as fertilised eggs, progress to veliger (planktonic) larvae, then metamorphose into their adult form and develop gills and palps. Predation and settlement affect the distribution of settling larvae (Peterson and Andre, 1980). The Tellinoidea are r strategists, investing no parental care (MacArthur and Levins, 1967).

The life span of *M. tenuis* is about five years (Tebble, 1966). *D. vittatus* lives for two to three years when growth is rapid, but with normal growth may have a life span of up to seven years (Gofas, 2013a). The longevity of *F. fabula* is four or five years (Salzwedel, 1979). *L. balthica* generally lives for 3 years (Gofas, 2013b) and *S. plana* has a typical lifespan of five years (Coelho *et al.*, 2006). Given a constant food supply, growth in bivalves is related to temperature, with species found in cold water thought to be longer lived (Abele *et al.*, 2009).

L. balthica has been noted to live up to twenty years in colder waters (Gilbert, 1973), most likely owing to the intermittent food supply.

1.3 Competition

An ecological niche is defined as the ecological role of a species in an ecosystem and the range of conditions which can facilitate its survival (Polechová and Storch, 2008). Determination of resource competition requires detailed knowledge of a wide range of processes which may be involved, including diet overlaps, prey selectivity and feeding efficiency (Kellnreitner *et al.*, 2013).

In bivalve communities, interspecific competition, although weak between coexisting species, is characterised by the following features: primitive behaviour patterns, limited energy expenditure, generalised feeding habits, ability to endure long periods of near-starvation, and widespread limitation of population densities by physical disturbances and intense predation (Stanley, 1973). There are many types of competition in marine communities (Levinton, 1982): competitive exclusion by exploitation is the principle difference between deposivore and suspensivore communities, with this particular form of exclusion very unlikely among suspensivores (Levinton, 1972). Exclusion by exploitation involves the consumption of resources thus rendering them unavailable for other organisms. Owing to the nature of the suspended seston resource, moving relatively rapidly with tides and currents, depletion of available food by nearby organisms only becomes significant in dense epifaunal beds such as mussel beds (Frechette *et al.*, 1989). Other forms of competition include: interference, which is not thought to be significant between Tellinoids, and competition for space, a driver of competition among suspensivores. The nature of the competition can be direct displacement, more efficient utilisation of the same resource or pre-emption (Levinton, 2009). More complex mechanisms include predation pressure on a resource competitor or transitive effects of resource utilisation. Resource partitioning is limited in many benthic communities owing to the significant effects of predation and physical disturbance (Stanley, 2008). As a result, absolute competitive exclusion resulting in extinction is uncommon, and dominance is frequently determined by early colonisation. This theory may account for why many species can coexist in habitats with fewer limiting resources than species (Tilman, 1994).

1.4 Approach

As little is known about the feeding ecology of Tellinoids in Dublin Bay, the factors which influence the nature and rate of bivalve feeding were examined.

Niche differentiation and division between the five species of Tellinoid found in Dublin Bay is the subject of this investigation, which builds on Yonge's (1949) morphological studies and on the work of Wilson (1990, 1976b, 1977, 1978, 1988, 1997) (e.g. Gill and palp morphology; Distribution and abundance; Tolerances; Resource partitioning; Density population structure and growth rate). Select aspects of the interactions between Tellinoid bivalves and their environment are examined alongside the implications for the short-term and long-term fitness of individuals, populations and ecosystems. In order to compare the five species of Tellinoid in Dublin Bay, sites were chosen to determine habitat preferences, assemblage, and environmental parameters. Internal morphology was examined in order to determine the ratio of palp to gill area and the quantification of metabolic processes was determined by bioenergetic and dietary studies.

1.5 Hypotheses

Three following hypotheses were tested to examine resource partitioning and feeding in five Tellinoid species:

1) H_1: There is a relationship between the dominant feeding mode of an assemblage and its biodiversity.

2) H_2: There is a relationship between feeding mode or feeding tendencies and palp to gill area ratios, positive in respect of deposit feeding tendencies. (Chapter 3)

3) H_3: Resource partitioning occurs in deposivores but does not occur in suspensivores (*i.e.* within suspensivorous groups all species occupy the same niche and suspended particle capture efficiency is the same, while this is not the case for deposivores). (Chapters 4 and 5)

4) H_4: There is a discernible difference in the feeding efficiency, i.e. feeding efficiency energetics and assimilation, between deposivores and suspensivores. (Chapter 6)

In H_1 it is expected that deposivorous assemblages have greater biodiversity than suspensivorous assemblages (Levinton, 1972).

In H_2 Palp to gill area ratio was determined by direct measurement of these anatomical structures. As palps are used to sort ingested material, the greater the volume which needs to be sorted internally, the larger the palps. A small palp:gill area ratio was expected to indicate

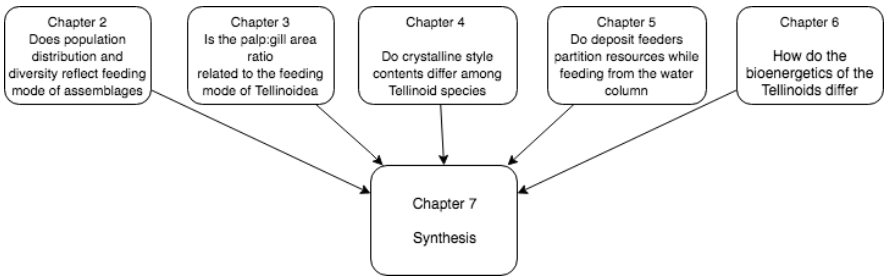


Figure 1.7. A diagrammatic view of thesis chapters. Each chapters covers distinct aspects of Tellinoid biology.

suspension feeding, as in *Mytilus edulis* an obligate suspensivore (Kamermans, 1994).

In H_3 Resource partitioning was tested for all species, and, if Levinton's (1972) hypothesis held true, deposivores would exhibit partitioning of available resources by preferential ingestion, while suspensivores would not. Suspended particle capture efficiency preference was measured using a Coulter Counter, and crystalline style analysis, as a proxy for stomach contents, which provided a comparison of ingested diet among species.

In H_4 Scope for Growth (Widdows and Staff, 2006) was used to determine the potential for growth and reproduction of the bivalves. If the results were to suggest that feeding economies differ between species, then this metric could represent an alternative indicator of competitive advantage to filtering rate alone. Scope for Growth was used to test the advantages and disadvantages of different modes of feeding *i.e.* the utilisation of different food sources and the determination of any resultant potential competitive advantage. Gut time passage and chlorophyll concentration provided metrics with which to compare resource processing between the species.

1.6 Thesis outline

This research adds to knowledge of the biology and ecology of the Tellinoidea in areas relating to feeding interaction, species distribution, dietary overlap, prey selectivity and bioenergetic potential (Figure 1.7). The ecological principles being tested are competition, niche width and resource partitioning.

This thesis is divided into the following components: background and rationale (Chapter 1); Descriptive field characteristics of where the bivalves are found in relation to environmental variables and other organisms (Chapters 2). Patterns and field observations are very

important (Underwood *et al.*, 2000); Feeding mode determination through physical characteristics, the examination of palp area to gill area ratios (Chapter 3); Determination of niche width in terms of ingested food analysis and particle sizes (Chapters 4 and 5); Ecophysiology of bivalves including physiological indices for comparison of energetics among the five species (Chapter 6); Finally a discussion and conclusion of findings (Chapter 7).

1.7 Aims

This thesis was the first study focused on a single bivalve superfamily in terms of feeding niche differentiation and classification, it aimed:

To determine where the littoral Tellinoids are found in relation to each other and environmental variables in Dublin Bay.

To determine the palp:gill area ratios of Tellinoids from Dublin Bay in order to better define feeding type.

To establish niche width in terms of particle size using dietary analysis and particle size ingestion analysis.

To determine bioenergetic and physiological indices for the littoral Tellinoidea in Dublin Bay.

This work advanced the understanding of the ecology of littoral Tellinoids in Dublin Bay. Field distribution and abundance metrics of Dublin Bay's macrofauna revealed little temporal change in the ecosystem. The field of experimental marine biology was advanced by the development of novel techniques, namely; determining the area of bivalve internal feeding organs using photographic methods and diet composition determination by crystalline style analysis. Levinton's (1972) hypothesis that deposit feeders tend to partition resources to a greater degree than suspension feeders was not evidenced by experimental results, however a consequence of the hypothesis *i.e.* greater deposivore assemblage diversity, was apparent. The outcomes of the feeding type determination, using palp to gill area ratio, can be applied to future network analyses, using feeding guilds, of Dublin Bays ecosystem, providing a basis for evidence-based conservation objectives.

Chapter 2

Distribution, Abundance and Biomass of Tellinoids in Dublin Bay

Abstract

Intertidal benthic macrofauna was sampled at 46 stations (2 replicates per station) along transects at three sites in Dublin Bay (Bull Island, Blackrock, Sandymount; Dublin city), and one in Balbriggan (Gormanstown Beach; North county Dublin). Tellinoids were found to constitute 32% of the total biomass of all macrofauna. Bivalves comprised 85% of the total biomass and *Cerastoderma edule* and Tellinoids accounted for 51% and 37% respectively of biomass of bivalves. Individual Tellinoid species were associated with distinct biotopes: *M. tenuis* was found at most stations and especially abundant in cleaner, sandy areas; *L. balthica* and *S. plana* in muddy sand; *D. vittatus* and *F. fabula* were found separately in clean sandy habitats around low water. Shannon (1948) Diversity Index (H) for bivalves, an integrated measure of species richness and evenness, values ranged from 0.39-1.27, and were higher in silty sites containing *S. plana* and *L. balthica* than those containing *F. fabula*, *D. vittatus* and abundant in *M. tenuis*. Abundance-Biomass Curves for bivalves indicated mild to moderate disturbance of the sites (Warwick, 1986), with Sandymount's W-statistic, a proxy for the degree of disturbance of a habitat, derived from the Abundance-Biomass Curve (Clarke, 1990), indicating least disturbance.

2.1 Introduction

In order to categorise the niche a bivalve inhabits, it is necessary to study their distribution and abundance in the field, and the influence of environmental characteristics on this distribution (Green, 1971). Species distributions are affected by interactions of physical environmental variables and sediment characteristics, and distribution patterns can suggest whether one species may have an effect on the distribution of another. Establishing baselines by field observation, and understanding the patterns encountered is of critical importance (Underwood *et al.*, 2000). Important factors in determining the distribution of bivalve species in Dublin Bay include tidal height and sediment grain size, with small grain size being associated with a higher organic fraction and the presence of deposit feeders (Roth and Wilson, 1998). Chemical cues, such as carbonate saturation level, also affect not only the selection of a site for settlement by bivalve larvae, but also their survival rates once settled (Green *et al.*, 2004). Biological cues such as the presence of diatom films can also induce the active selection of a site for settlement (*e.g. L. balthica* larvae; (Van Colen *et al.*, 2009)). Juveniles of *L. balthica* have, however, also been observed to migrate shore-wards and subsequently seawards during their development (Beukema *et al.*, 1993). Structure of marine macrobenthos varies at geographical scales; in European waters, Sokołowski *et al.* (2012) found total abundance values ranging from 63 to 34,517 individuals per m^2, with 3-166 species recorded, Shannon (1948) diversity indices (H) of $0.26-3.26$ (Margalef, 1957) and Pielou's (1966) evenness index of up to 0.73. Here, as in other studies focusing on bivalves (Whiteley and Bendell-Young, 2007; Lees and Driskell, 2007) Shannon (H) and Pielou indices are calculated for the bivalve community, to allow comparability with other bivalve studies *i.e.* comparing the entropy of each bivalve of one bivalve community with the entropy of each bivalve in another bivalve community (Whiteley and Bendell-Young, 2007; Wu, 1982).

2.1.1 Description of study area: Dublin Bay

UNESCO Dublin Bay Biosphere was designated in 2015 owing to its distinctive ecological habitats and biodiversity (Murphy *et al.*, 2016). North Bull Island and Sandymount Strand are RAMSAR sites within the UNESCO Dublin Bay biosphere site. Dublin Bay lies at the mouth of the River Liffey (Figure 2.1). The main influence is from the Irish Sea, with inflows from the Liffey, Dodder and Tolka rivers.

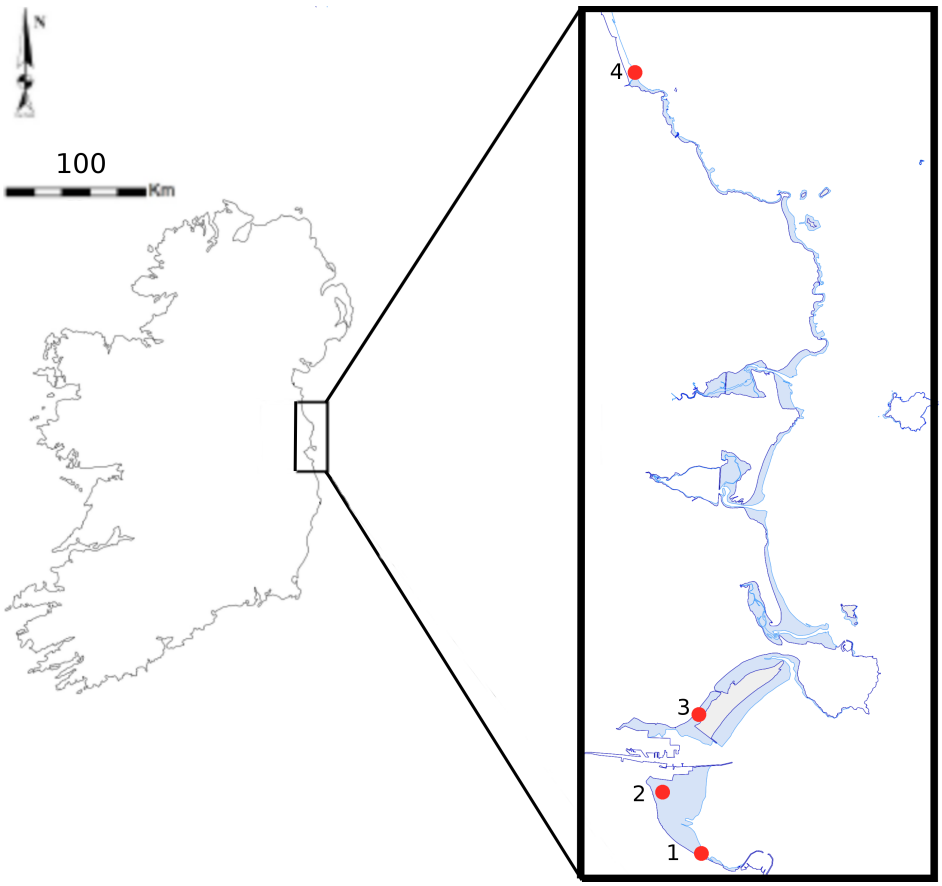


Figure 2.1. Map of Ireland showing the location of the sampling area, insert shows sampling sites labelled with red dots. 1: Blackrock, 2: Sandymount, 3: Bull Island, 4: Balbriggan. 1, 2 and 3 are within Dublin Bay. Map credit Ordinance Survey Ireland (2017).

The bay has a water turnover rate of 3.57 days and encloses an area of about 296km^2 with the intertidal zone accounting for 18.6 km^2 (Wilson *et al.*, 2007). The water quality is generally good, and the bay is relatively sheltered from the predominantly western winds owing to its eastern aspect (Brooks *et al.*, 2016). The subtidal benthic area varies in depth from 5m depth in the inner area to 25m further out (Mansfield, 1992). It is a shallow, sandy bay protected from major wave disturbance of the sea floor by both the linear offshore sand banks and land surrounding it (Walker and Rees, 1980).

The intertidal area of the bay is mostly sandflats alongside mudflats, and includes a range of coastal, intertidal and subtidal habitats and has wetlands that are home to internationally important populations of birds. It acts as a nursery area for fish species harvested from the Irish Sea (Brooks *et al.*, 2016). Population densities of infaunal invertebrates, other than bivalves, are low (Wilson, 1982a), yet the bay supports large numbers of overwintering

wildfowl.

2.1.2 Study sites

This study was conducted in three sites in Dublin Bay, (Blackrock, Sandymount and Bull Island) and one site in North Dublin (Gormanstown beach, Balbriggan).

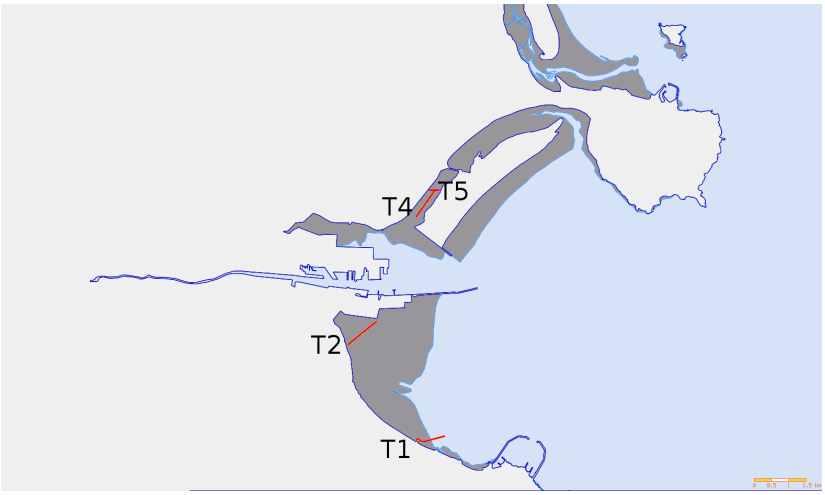


Figure 2.2. Map of Dublin Bay showing low and high water marks along with intertidal region show in grey. Low water mark is shown by a light blue solid line, high water mark is shown by a navy solid line. Transects shown by orange line. Map credit Ordinance Survey Ireland (2017).

The four sites were chosen as they are known to collectively contain all five Tellinoid species found in Dublin Bay. The mean low water mark of Dublin Bay is crossed by Transect 1 at Blackrock, but not Transects 2 and 4 at Sandymount and Bull Island (Figure 2.2), while Transect 3 crosses the low water mark at Balbriggan (Figure 2.3). Balbriggan was chosen as an additional study site as it hosts a large community of *D. vittatus* alongside a strong population of *M. tenuis*. The main inflow in Balbriggan is the Delvin river. The site is less sheltered than Dublin Bay. This site was included in order to study *D. vittatus*, as the abundance of the species in Dublin Bay was too low at the time of this investigation.

Stations were positioned at a spatial separation of approximately 50m. The sampling was planned to include each habitat type at each particular site.

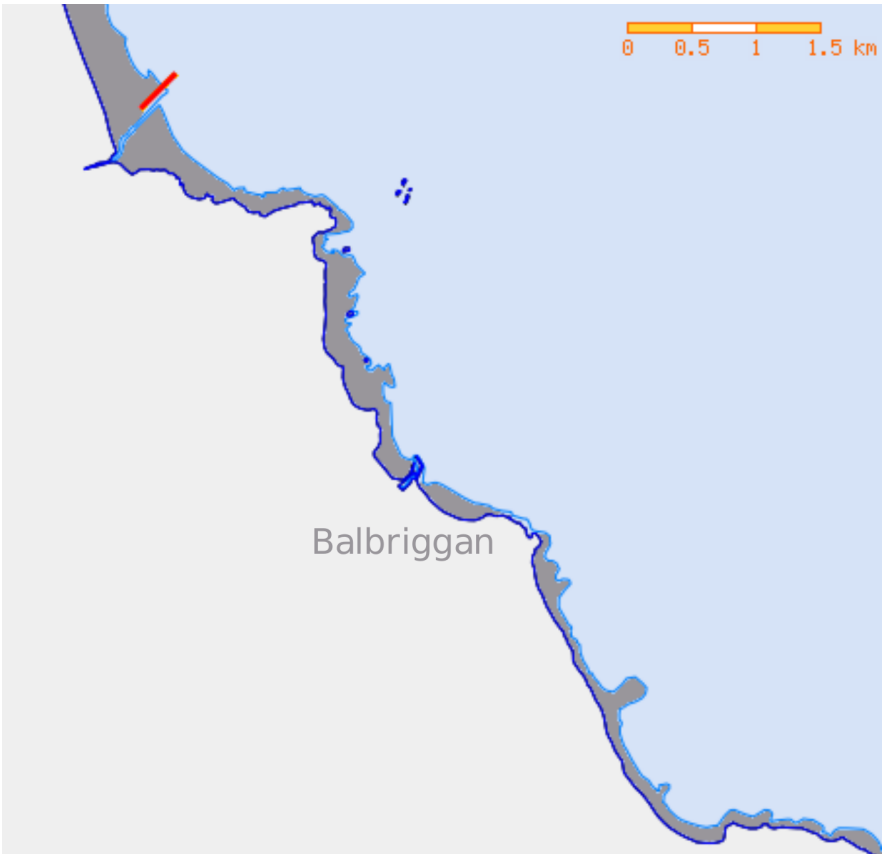


Figure 2.3. Map of Gormanstown, Balbriggan showing low and high water marks along with intertidal region show in grey. Low water mark is shown by a light blue solid line, high water mark is shown by a navy solid line. Transect shown by orange line. Map credit Ordinance Survey Ireland (2017)

2.1.3 Dublin Bay: A previous study

A comprehensive and detailed investigation of the macrofaunal distribution and abundance of Dublin Bay was recorded by Wilson (1982a), in which it was noted that bivalves dominated the standing biomass, with *M. tenuis* being the second most dominant bivalve species. The Dublin Bay intertidal was sampled using a systematic grid based sampling pattern.

Considering the Bay as a whole, *M. tenuis* was found in approximately half of the samples, including high abundances near the South Wall to the east of Blackrock, but almost no individuals were found to the west of Bull Island. *F. fabula* was found in small numbers near the low water mark off Bull Island, considerably more abundant near the Low Water Mark (LWM) close to Blackrock, but apart from this, only a small number of isolated individuals

were encountered, all on the South side of the bay. *D. vittatus* was found in low numbers close to the LWM.

L. balthica was found behind Bull Island and on Sandymount strand. Abundances were particularly high in the shelter of Bull Island, at intermediate tidal height. On the South side of the bay abundances were concentrated towards Ringsend, with two stations of exceptionally high abundance, one in a large tidal creek, and three stations of moderate abundance near the High Water Mark (HWM) at Sandymount, along with scattered individuals. The distribution of *S. plana* was similar, albeit more restricted to the sheltered creeks near Bull Island, and a small number of individuals on the South side of the bay, with one station showing higher abundance which coincided with the high abundance of *L. balthica*.

S. plana frequently coincided with *L. balthica* and was only found in five stations without *L. balthica*, which had a much greater range. The range of *F. fabula* overlapped to a large degree with that of *D. vittatus*, co-occurring in the same samples particularly where *F. fabula* were abundant. *M. tenuis* co-occurred with *F. fabula* frequently, but not in the stations where *F. fabula* were abundant. *F. fabula* are abundant in the Dublin Bay sublittoral and are thought to have increased in abundance along with the nut clam *Nucula turgida* owing to changes in mud composition following the cessation of dredge spoil dumping (Walker and Rees, 1980). *M. tenuis* was effectively absent from the range of *L. balthica* on the North side, but co-occurred to a reasonable degree on the South side, albeit with lower abundance of *M. tenuis* than elsewhere (Wilson, 1982a).

2.1.4 Investigation background

While approximate species composition and distribution of Tellinoid bivalves in Dublin Bay may be known locally, accurate estimates of abundance and biomass for the present day, since Wilson's (1982b) 1977 study, are generally lacking. As well as estimating the abundance of bivalves in sample areas of the bay, the investigation included the relationship between assemblage and habitat characteristics. The niches that bivalves inhabit are illustrated by the results of the investigation. For each Tellinoid, the bivalves with which they overlap in niche were determined. The presence or absence of Tellinoid species and the composition of their bivalve communities were documented. A comparison of shell thickness with sediment composition was also undertaken.

Determining distribution, abundance and population structure aids understanding of potential competitive interactions between the Tellinoids in Dublin Bay. Population structure

and patterns need to be characterised before processes can be identified (Underwood *et al.*, 2000). In Blackrock, Co. Dublin, *F. fabula* is found at the mean low water mark and below (sublittoral), whereas *M. tenuis* is found from mean low water mark up to the mean high water mark (littoral) (Wilson, 1990). This distinct distribution of *M. tenuis* and *F. fabula* has been noted elsewhere, particularly in Kames Bay in Scotland (Stephen, 1928; Watkin, 1942; Clark and Milne, 1955; Wilson, 1990). Bivalves account for 80% of the biomass in Dublin Bay in 1977, and are a highly important component of the Dublin Bay system (Wilson, 1982b).

Part of this investigation involved establishing the nature of the assemblage. It included the identification of physical, environmental traits associated with low or high biomass, abundance, dominance and diversity of bivalves, particularly Tellinoids. Wilson's (1982a) study was larger in scale than the study in this thesis and had a different sampling design, so is therefore not directly comparable statistically.

2.1.5 Niche overlap

A fundamental niche is modelled as existing in a multi-dimensional space (Hutchinson, 1957), representing the conditions in which a species can survive and reproduce. No two species can occupy precisely the same niche, as the "better adapted" species will eventually dominate, regardless of initial concentrations (Gause and Witt, 1935). Two species can, however, occupy niches effectively, distinguished only by their physical separation from one another. Grinnell's (1917) definition of niche, as the places where a species is found, is a subset of Hutchinson's (1957) hypervolume defining potentially suitable habitats. Sympatric species must differ in at least one dimension, such as diet, or the dominant species will always eventually outcompete the other. Niche overlap and differentiation can be expressed both geographically and in terms of other factors such as feeding preferences *i.e.* size and morphospecies of algae ingested. More recently, Hubbell (2001) took an alternative view, hypothesising that within a community of similar species, the success or otherwise of each species owes little to its adaptation to the environment, and that random changes in community rank of species are common. Physical factors, including sediment composition, height above tide, organic content of sediment and locations within the bay, are further components of species' niches. The realised niches, as revealed by this investigation of the Tellinoids of Dublin Bay, are restricted to the portion of their fundamental niches in which the species can compete with the other species present.

2.1.6 Abiotic factors

Abiotic factors of potential significance to the distribution of Tellinoids are: salinity, sediment type, redox potential discontinuity layer depth (RPD) (cm), height on shore, sediment temperature and water temperature. Sediment type is particularly important as distinct faunal communities are commonly associated with particular types of sediment (Davis, 1925; Thorson, 1957). The size of sand grains in a substrate is important in determining the distribution of species (Bacescu *et al.*, 1971) and also has an effect on the settling and metamorphosis of bivalve larvae (Gray, 1967). RPD depth is typically related to an interaction of sediment size, turbidity and biota, with littoral sediment experiencing greater wave disturbance and hence oxygenation than sublittoral. Finer, silty sediments tend to be more cohesive than sandy substrates, with a diminished impact of surface hydrological conditions below the top layer of sediment (Riedl *et al.*, 1972). Benthic biota influence the porosity and cohesiveness by secreting binding agents and disturbing the sediment. In times of increasing oceanic hypoxic conditions, the RPD depth may also be used as a metric of habitat quality, when other factors have been accounted for (Gerwing *et al.*, 2015). Mature undisturbed communities tend to have higher dominance indices in terms of biomass than abundance, with this relationship inverted in the case of grossly polluted locations, so the degree of greater (or lesser) dominance can be used to infer the level of disturbance at a site (Beukema, 1988; Warwick, 1986).

M. tenuis and *F. fabula* are mainly found in clean sand (Holme, 1949) whereas *S. plana* is commonly found in muddy substrate (Barnes, 1973). The key abiotic factors found previously in Dublin Bay were tidal height and sediment type (Roth and Wilson, 1998).

2.1.6.1 Shell thickness of Tellinoids

Several factors influence the suitability of a habitat for a given species. Sediment type is relevant for a number of reasons, including the ability of bivalves' palps to sort their food in the presence of fine sediment, if applicable. Shell thickness is another factor, which may limit a bivalves' ability to survive and colonise a habitat. Possessing and maintaining a thick shell is an expensive requirement, and a species is unlikely to evolve a thick shell unless it confers a commensurate advantage. *Mytilus edulis*, when translocated to areas subject to predation by crabs, grow thicker shells, exhibiting phenotypic plasticity (Leonard *et al.*, 1999). In the Tellinoids, predation is of greater concern for shallow-dwelling species, such as *D. vittatus*, which is found almost exclusively in the top 5 cm of sediment (Beukema, 1974), and *L. balthica*, which typically burrows 2 cm deep in summer and 5 cm deep in winter, than for

deep burrowing species such as *S. plana*, which burrows 7-12 cm (or more), as predation by birds is limited by beak length (Zwarts and Wanink, 1993). *M. tenuis* is deeper burrowing than *F. fabula*, with the latter not found below 10cm, while some *M. tenuis* are found below 15 cm (Wilson, 1979). Differences in shell thickness, which are not accounted for by likelihood of predation may be related to sediment composition. Previous studies on shell thickness in bivalves are sparse. Shell thickness has previously been measured in fresh-water bivalves (Unionidae) measuring perpendicular to the plane defined by the nacreous plates (Dettman *et al.*, 1999). As measurements of the shell thickness at various points perpendicular to the nacrous layer varied by over 50 % on individual specimens (Dettman *et al.*, 1999), the particular method was not considered sufficiently descriptive here and an alternative system was implemented.

2.1.7 Aims

The objectives of this investigation were:

- To map and characterise the distribution and abundance of Tellinoids in Dublin Bay in known areas of Tellinoid abundance;
- To determine how the distribution of bivalves in Dublin Bay is influenced by:
  - (1) Tellinoid species
  - (2) abiotic factors
- To examine shell thickness in relation to sediment type.

This investigation will test the following hypotheses:

H_1: There is a relationship between environmental factors including sediment and the feeding mode of communities living in that habitat.

H_2: Tellinoid deposivore communities have greater diversity (measured by H) than suspensivore communities.

2.2 Methods

An investigation of benthic macrofauna was conducted to determine the distribution of Tellinoids in Dublin Bay, along with their niche divisions. Locations of transects were chosen to represent both the North and South of Dublin Bay. The transects (and thus sampling sites) were located in dynamic and non-dynamic areas. Transect locations were subjectively

chosen as representative areas which matched the criteria set out in the sampling framework (Section 2.2.1). Transects were used as they are appropriate for distribution studies, particularly where a known habitat gradient exists, or a habitat boundary is to be crossed (Wilson, 1982b). At each site, a transect was established to assess the abundance of organisms systematically, at regular intervals, these points where two replicates samples were taken are referred to as stations. Density estimates for organisms were quantified by extrapolating to a metre squared density from two $400cm^2$ samples at each station.

2.2.1 Sampling framework

Sampling took place from the 20^{th} to the 23^{rd} July 2012 at low tide. Sampling stations along transects were non random, they were approx 50 m apart from each other. Transects were selected where practical to cover the maximum range between low (spring tide) and high water marks at the locations while covering known distributions of bivalves. Stations were marked using Global Positioning System (GPS) co-ordinates geo-linked to Google maps. Sampling frameworks were positioned as follows:

- Blackrock: Starting at the high tide mark and ending at spring low tide mark, avoiding an eddy associated with tidal flow (Figure 2.4) (Transect 1).
- Sandymount: Starting at the spring low tide mark and ending at high tide mark (Figure 2.5) (Transect 2).
- Balbriggan: Starting at spring low water mark and continuing towards high tide mark perpendicular to the shore (Figure 2.6)(Transect 3).
- Bull Island: As this area is sheltered from direct contact with the open sea and therefore impossible to sample from low tide to high tide, the area was covered using two transects. One transect ran parallel to the water flow, the other perpendicular across the water flow (Figure 2.7) (Transects 4 and 5 respectively).

Two replicate samples were collected at each station on transects, each station was approximately 50m apart. A total of 92 samples were taken and analysed. The sites were chosen as they were know to contain populations of Tellinoids. The number of stations on each transect varies, stations were included in order to best represent the population of an area from one point to another.

Figure 2.4. Sampling plan from Blackrock showing study stations labelled with yellow pegs (Transect 1). Station numbers are 1-17, increasing towards the East. Mean low water mark (MLW) (is shown by a light blue solid line, high water mark is shown by a navy solid line. Some samples were taken near spring low water, below the mean low water mark. Map credit Google maps (2017); Tide marks Ordinance Survey Ireland (2017)

Figure 2.5. Sampling plan from Sandymount showing stations labelled with yellow pegs (Transects 2). Station numbers are 18-26, increasing towards the North-East. Map credit Google maps (2017)

Figure 2.6. Sampling plan from Balbriggan showing study stations labelled with yellow pegs (Transect 3). Mean low water mark (MLW)is shown by a light blue solid line, high water mark is shown by a navy solid line. Station numbers are 37-46, increasing towards the North-East. Map credit Google maps (2017); Tide marks Ordinance Survey Ireland (2017).

Figure 2.7. Sampling plan from Bull Island showing study stations labelled with yellow pegs (Transect 4 and 5). Station numbers are 27- 31 increasing from West to East, then 32-36 increasing towards the South-West. Map credit Google maps (2017)

2.2.2 Abiotic measurements and sample collection

Sediment temperature at five cm depth, Global Positioning System (GPS) co-ordinates, RPD (Redox-potential discontinuity) depth and salinity (measured using a refractrometer) were recorded for each station. A sample of sediment was also taken using a 60 ml corer (110 mm length, 26.5 mm diameter). A faunal sample was taken from each replicate using a plastic corer (18 cm depth, 22 cm diameter), the core was then sieved using a 1 mm mesh sieve. The fauna remaining in the sieve were transferred to a pre-labelled container. All samples were returned to the laboratory within six hours and placed in a solution of 10% formalin. Rose bengal was added to the faunal containers to stain live specimens (living tissue) pink.

2.2.3 Analyses of abiotic factors: sediment composition analysis

Sediment samples were pre-treated (Section 2.2.3.1) and the <500 μm fraction processed to determine particle size distribution using laser diffraction (Section 2.2.3.2).

2.2.3.1 Pre-treatment of Sediment Samples

Sediment samples from cores were transferred onto pre-weighed aluminium foil strips in the lab. The samples were dried in an oven at 100 °C±5 °C for 24 hours and weighed to determine dry weight. To determine loss on ignition and the organic matter content, sediment samples were placed in a furnace at 450 °C for 6 hours (Bale and Kenny, 2005). Ash weight after ignition was subtracted from dry weight, providing an estimate of total organic matter content (ash free dry weight). Each sediment sample was removed from its pre-weighed aluminium foil, and shaken through a series of sieves (*i.e.* mesh size 8 mm, 4 mm, 2 mm, 1 mm and 0.5 mm) for granulometric analysis. The contents of each sediment fraction were weighed and the under 500 μm component weighed. Two subsamples of the <500 μm fraction were prepared for laser diffraction particle size analysis.

2.2.3.2 Particle size analysis using laser diffraction

Two <500 μmm fraction subsamples, of mass 5 g for sandy sediments, 2 g for muddy sediments owing to their greater turbidity in suspension, and hence greater obscuration of the laser, were placed in individual 250 ml conical flasks. 100 ml of 10 % sodium hexametaphosphate was added and the mixture was shaken by hand, prior to analysis, to ensure the even dispersal of particles throughout the solution. Before using the particle size analyser (Malvern Mastersizer/E laser) a blank measurement was taken, which consisted of a solution of sodium

hexametaphosphate (10 %). Sediment <500 μm fraction samples were added to 900 ml MilliQ water (filtered using a 0.5 μm filter) in the Malvern laser particle size analyser. Before obtaining results it was important that the obscuration measurement from the machine was within the ideal range of between 5 % and 20 % (Jones, 2002). If this could not be achieved by changing mixing settings, appropriate amounts of water (5 ml at a time) or sediment (0.5 g) were added to the solution, until the machine indicated a reading was possible. Three readings were taken for each sample.

Taking into account the material remaining in the sieves and the results of the laser diffraction, the proportion of the material comprised of particles >2 mm, between 63 μm – 2 mm, and <63 μm were converted into percentages of the total sediment weight. Sediments were classed as mud, muddy sand and sandy mud based on the ratio of mud (< 0.063 mm) to sand (> 0.063 mm) in the <500 μm material i.e. 9:1 (mud), 9:1 – 1:1 (sandy mud) and 1:1 – 1:9 (muddy sand) (Folk, 1954).

2.2.4 Analysis of biota: faunal sample analysis

The biota from each sampling station were processed separately. Faunal samples, fixed in 10 % formalin, were placed in sorting trays and all living matter, (living at the time of sampling), removed. The material was then classified, with all macrobenthos collected identified to the lowest taxonomic level practical and processed in the same manner. Bivalves were identified to species level. The total quantity of each species of bivalve in each sampling station were wet weighed to ±0.01 mg using a calibrated Mettler Toledo B154-S analytical balance after blotting the animal on tissue paper. Individuals of bivalves were counted, measured (shell length (mm), shell depth (mm) and shell width (mm) were recorded with a Vernier callipers (to 0.01 mm) and placed in an oven at 105 °C ±5 °C for 24 hours. The samples were left to cool in a desiccator, reweighed, and placed in a furnace at at 450 °C for 6 hours in order to determine loss on ignition and hence organic matter content (ash free dry weight) (Bale and Kenny, 2005).

2.2.5 Shell thickness of Tellinoids

A programme of shell measurement was developed; shell thickness was measured with a modified vernier callipers (Figure 2.8) on the intersection of two lines; one drawn from the posterior margin to the anterior margin and the other drawn perpendicular to this line, through the umbo (Figure 2.9). The right hand valve from each specimen was measured, although it must

be noted that both valves in the Tellinoids may vary in thickness and form (e.g. In *F. fabula* the right valve has wavy striations). This measurement point was located at a flat point on the shell, and was appropriate for comparison across species. Specimens for shell thickness analysis were taken from the stations characteristic for each species, *i.e.* where the species was most abundant. (Pincer callipers were not sufficiently accurate, as accuracy to two

Figure 2.8. Vernier callipers, modified with copper wire, used to measure shell thickness.

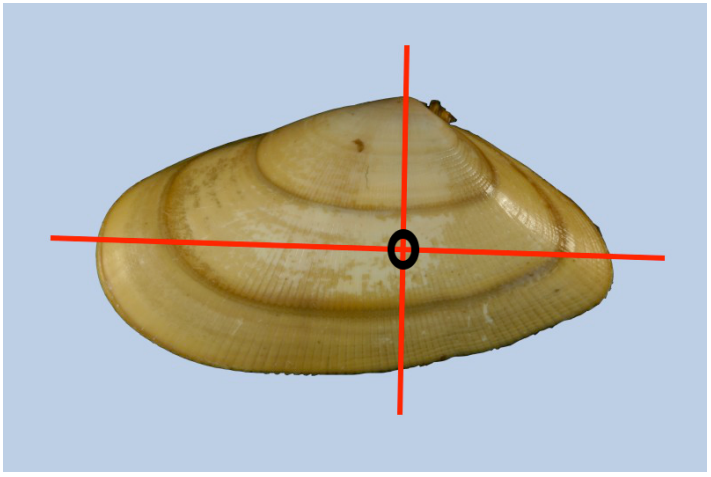


Figure 2.9. The Location of the measurement point for shell thickness on a *D. vittatus* valve (Photo modified from Wilkinson (2010))

decimal places were required, and unmodified vernier callipers are not capable of measuring across the surface of a curved shell owing to their flat jaws, so a modified callipers were developed. This callipers were self calibrating and were checked against known measurements). The bivalves measured for shell thickness comparison were collected from stations where the

particular species were found in high abundance, with associated sedimentary characteristics recorded.

2.2.6 Data Analysis

Data was visually examined using Excel (Microsoft). PRIMER–E (Clarke, 2006) and R (R Core Team, 2016) were used to carry out data analyses. The similarity of stations based on normalised euclidian distance of environmental factors was carried out. Bray Curtis similarity of total biomass was used and separately Bray Curtis similarity of bivalve abundance. BEST analysis was carried out in order to determine correlation between environmental variables and bivalve species presence or absence. Dominance and abundance biomass comparisons were carried out for each site and bivalve. Evenness and diversity indices were carried out for each site for bivalves. A regression of shell thickness against length and species was carried out. Plots of abundance were superimposed on Google maps using R plotgooglemaps package available on CRAN. PERMANOVA, PERMDISP, SIMPER and MDS plots were generated in R.

2.3 Results

2.3.1 Environmental variables

The environmental conditions for the sites at which each species were most dominant was considered characteristic for that species. For *M. tenuis*, which was abundant at several stations, the characteristic environment was considered to be where it was abundant but other Tellinoids were not, in the mid-shore at Blackrock. These characteristic environmental conditions separated *S. plana* and *L. balthica* from the other Tellinoids. The key abiotic factors noted by Roth and Wilson (1998) in Dublin Bay were sediment type, which in this investigation distinguishes the locations containing *L. balthica* and *S. plana* from the others, and tidal height, which closely agrees with the changes in relative abundances of *F. fabula* and *D. vittatus* with respect to *M. tenuis*. *F. fabula*'s location was also distinguished by low sediment organic content and a shallower RPD than for *D. vittatus* and *M. tenuis* (Table 2.1). Sediment type classifications for each site based on the <500 μm fraction also separated *L. balthica* and *S. plana* from the other Tellinoids (Table 2.2).

Similarity of stations by environmental variables was not completely determined by location, although the locations in Bull Island were almost separated into two clusters apart

Table 2.1. Environmental conditions for sampling location most dominated by each Tellinoid species (Fine Gravel (>2 mm), Sand, Silt (<63 μm) and Organic fractions expressed as % of sediment.

Species	Fine Gravel	Sand	Silt	Organic	RPD(cm)	salinity	Tidal Height
L. balthica	0.0185	88.125	11.85	0.195	2	20	Mid
S. plana	0	90.395	9.605	0.315	2	21	Mid
F. fabula	0.038	97.515	2.445	0.057	8	38	Low
M. tenuis	0.661	97.12	2.22	0.2185	20	34	Mid-Low
D. vittatus	0.5325	96.935	2.53	0.232	20	35	Low

Table 2.2. Sediment classification of characteristic locations of each species (Folk, 1954).

Species	Sediment Type
L. balthica	Sandy Mud
S. plana	Sandy Mud
F. fabula	Sand
M. tenuis	Sand
D. vittatus	Sand

from the others - stations 22 and 24 from Sandymount were included in one of these clusters (Figure 2.10). Small clusters of individual stations occurred at a distance from the remaining data. One cluster included eight stations from Balbriggan and Blackrock, while the largest cluster included stations from Balbriggan, Blackrock and Sandymount. The clustering suggests that Bull Island is the most distinct in terms of environmental conditions, which may be owing to its status as a true estuarine location.

2.3.2 Abundance of Tellinoids

M. tenuis was found everywhere, except where there were large numbers of *S. plana* (Figures 2.11, 2.12, 2.13 and 2.14). *S. plana*'s preferred habitat appeared less suitable for *M. tenuis*, however there was some overlap in Sandymount where the species co-occur. *F. fabula* inhabited a very similar niche to *M. tenuis*, but preferred deeper waters. The relative proportions of *M. tenuis* and *F. fabula* is an indication of not only their relative preference, as species, for different physical niches, but also their competitive success in the presence of each other. *M.*

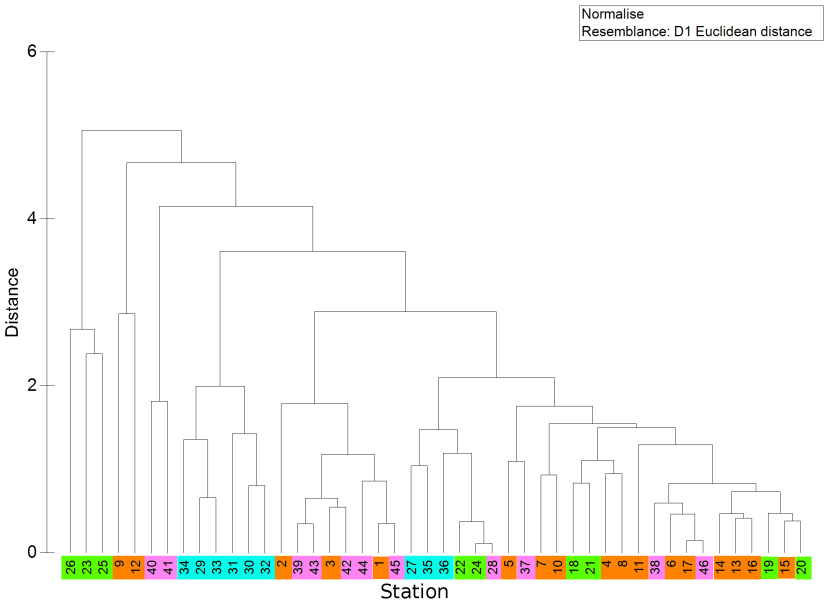


Figure 2.10. Similarity of stations, abiotic, environmental factors, based on the Euclidean distance of (Sediment type, Salinity, Organic content, RPD). Stations are labelled and colour-coded by site: Blackrock: Orange; Sandymount: Green; Bull Island: Blue; Balbriggan: Mauve.

tenuis were more dominant than *F. fabula* above the mean low water mark, *F. fabula* were more dominant than *M. tenuis*, albeit less dramatically, below the mean low water mark (Figure 2.11). There was no sudden distinction between the two populations of Tellininae, but rather a gradual shift towards higher numbers of one or the other. *S. plana* co-occurred with *L. balthica* . *D. vittatus* was found in extremely low numbers in Dublin Bay, but in high numbers in Balbriggan.

On the high shore in Blackrock (Figure 2.11), *M. tenuis* was dominant. Two individuals of *D. vittatus* were found in the midshore. The proportion of *F. fabula* increased from the midshore to the low water mark, with *F. fabula* being the most abundant species below the low water mark. No individuals of *S. plana* or *L. balthica* were found at Blackrock. Only one individual each of *Venus striata, Mya truncata, Cerastoderma edule*, and two each of *Venus verrucosa, Mactra correlina* were found at Blackrock.

Figure 2.11. Abundances of Tellinoids in Blackrock. The area of each circle represents the total abundance of Tellinoids at a station, with the segments of the circle presenting the relative proportions of each species. The orange circle is provided for scale and represents 100 individuals.

Sandymount's Tellinoid abundance (Figure 2.12) was not dominated consistently by any one individual species, although *S. plana* accounted for slightly over half of the individuals found. *S. plana* dominated the stations of high Tellinoid abundance, but was absent where *L. balthica* was dominant. *M. tenuis* dominated the inshore station, and one other station, while *L. balthica* was the most abundant species in two stations. At no site was abundance evenly distributed between the species (Figure 2.12). Other bivalves were also found in Sandymount, notably *Cerastoderma edule*.

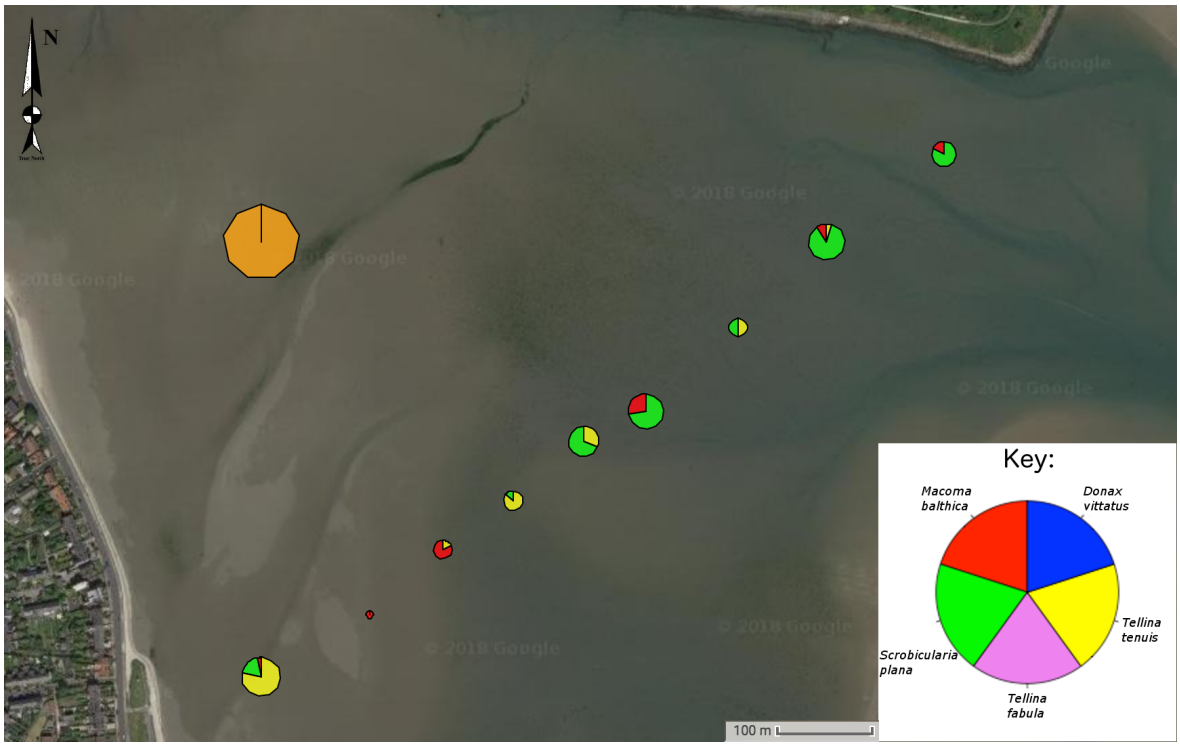


Figure 2.12. Abundances of Tellinoids in Sandymount. The area of each circle represents the total abundance of Tellinoids at a station, with the segments of the circle presenting the relative proportions of each species. The orange circle is provided for scale and represents 100 individuals.

A similar patterns of habitat division and overlap, between *M. tenuis* and *D. vittatus* was seen in Balbriggan as between *M. tenuis* and *F. fabula* in Blackrock, although *M. tenuis* was dominant throughout in Balbriggan (Figure 2.13), but the proportion of *D. vittatus* rose towards the spring low water mark, $< 5\%$ on the high shore to $20\% - 32\%$ of Tellinoids at the spring low water mark. No other Tellinoids were found in Balbriggan, and, of other bivalves, only 3 individuals each of *Venus verrucosa* and *Abra tenuis* were found.

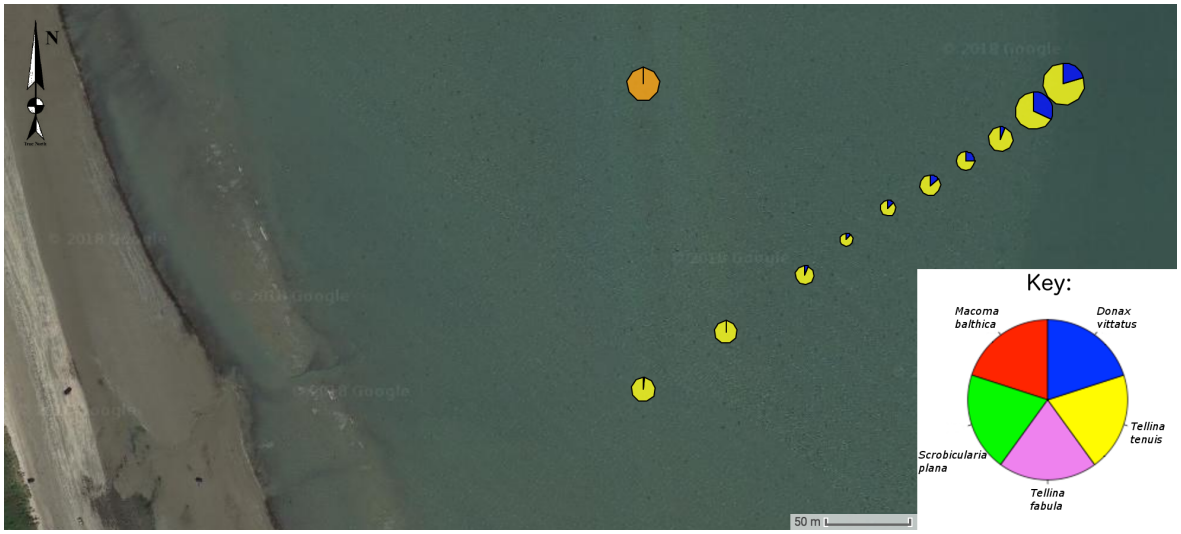


Figure 2.13. Abundances of Tellinoids in Balbriggan. The area of each circle represents the total abundance of Tellinoids at a station, with the segments of the circle presenting the relative proportions of each species. The orange circle is provided for scale and represents 100 individuals.

At Bull Island (Figure 2.14), *S. plana* was dominant, with *L. balthica* accounting for much of the residual abundance. *M. tenuis* was found at one station, co-occurring with *L. balthica* but not with *S. plana*. *Cerastoderma edule* and *Abra tenuis* were also found in substantial numbers, along with a single *Mya arenaria*.

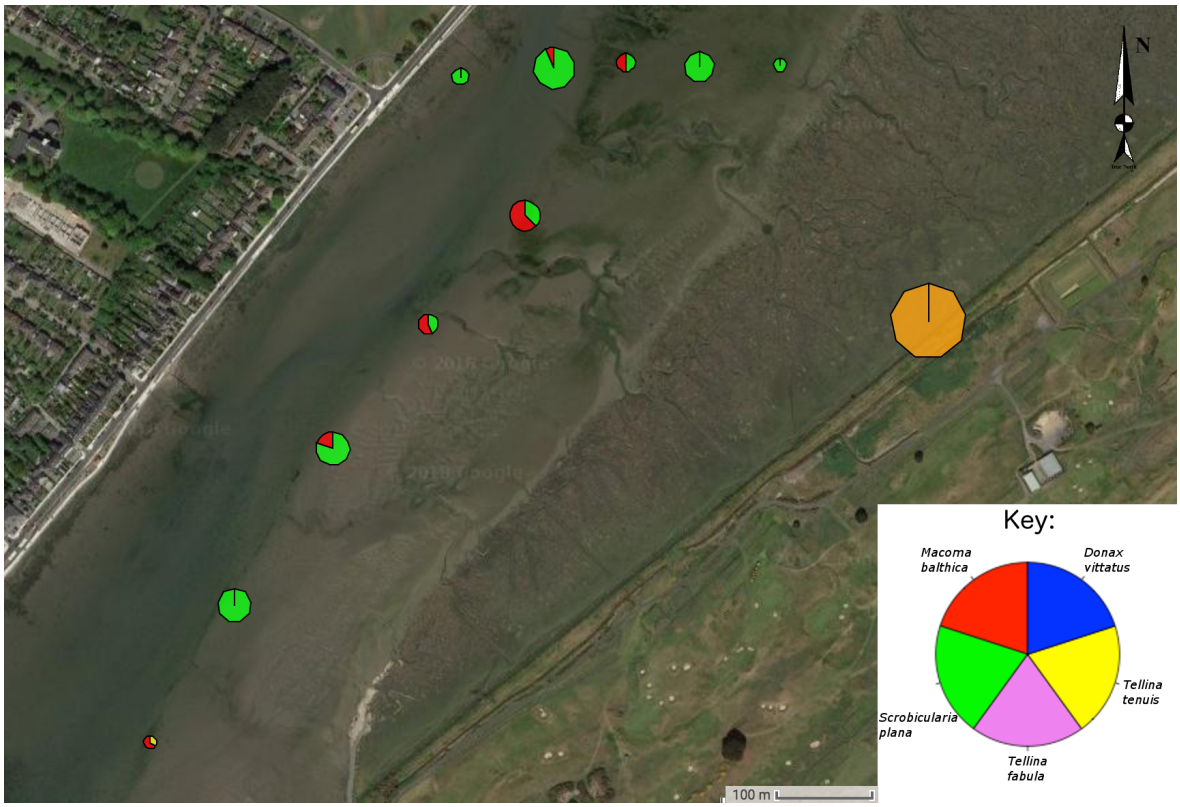


Figure 2.14. Abundances of Tellinoids in Bull Island. The area of each circle represents the total abundance of Tellinoids at a station, with the segments of the circle presenting the relative proportions of each species. The orange circle is provided for scale and represents 100 individuals.

2.3.3 Biotic similarity between stations

An analysis of similarity (Bray-Curtis) between sampling sites was conducted in Primer-E (Clarke, 2006) of biomass (ash-free dry weight) of all species found at each station (Figure 2.15). Bray-Curtis is a dissimilarity index used in the manner of a distance metric. The top level distinction separates Sandymount $(18-26)$ and Bull Island $(27-36)$ from Blackrock $(1-17)$ and Balbriggan $(37-46)$. Balbriggan's biota form a distinct group, more similar to each other than to any station in Dublin Bay. The biota of Sandymount and Bull Island are not clearly separated by biomass values, with two stations near the shore on Sandymount

being similar to most of those furthest from the sea at Bull Island, with the other stations in Sandymount and Bull Island being more similar to each other.

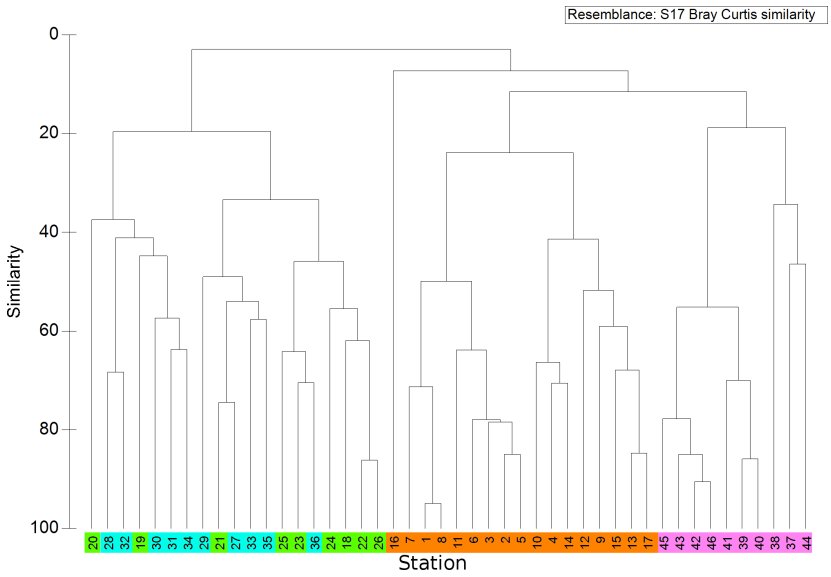


Figure 2.15. Bray Curtis similarity of stations by biomass (g AFDW) of all species of macrobenthos. The height of the linkage between stations indicates the level of similarity which distinguishes the groups linked. Stations are labelled and colour-coded by site: Blackrock: Orange; Sandymount: Green; Bull Island: Blue; Balbriggan: Mauve.

Owing to the presence of high abundance of small fauna, and several fragmented specimens, such as polychaete worms, a Bray Curtis analysis of similarity of abundance of all species was not practical. An analysis of similarity was also undertaken of the abundance of all bivalves found (Figure 2.16 on page 45). Stations in Blackrock and Balbriggan are again separated from those in Sandymount and Bull Island by the top-level distinction. Groups of stations from Balbriggan and Blackrock show greater similarity to each other in terms of bivalve abundance than to stations at the same site. For example, stations 37, 38 and 44, with high *M. tenuis* abundance and low *D. vittatus* abundance, are grouped with several stations in Blackrock, while the Blackrock stations with high *F. fabula* abundance (14-17) are distinct from the other Blackrock and Balbriggan stations. By contrast, the highest division between stations in Bull Island and Sandymount is almost unchanged from the biomass-based grouping, with sites 27 and 31 switching places.

A BEST analysis of correlation between the environmental variables and the presence/absence

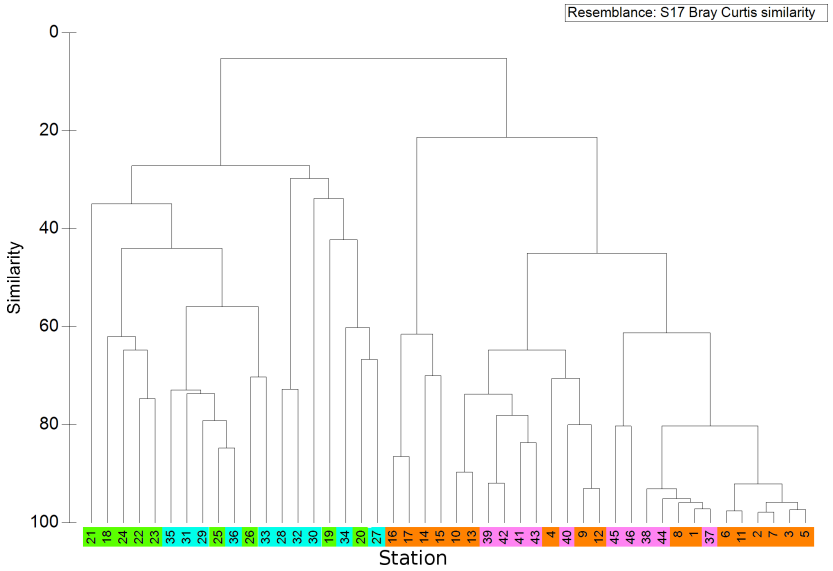


Figure 2.16. Bray Curtis Similarity by bivalve abundance. The height of the linkage between station indicates the level of similarity which distinguishes the groups linked. Stations are labelled and colour-coded by site: Blackrock: Orange; Sandymount: Green; Bull Island: Blue; Balbriggan: Mauve.

of bivalve species carried out using Primer-E indicated that the presence/absence of bivalve species was not random and associated with the environmental variables, (99 permutations, $\mathbf{p < 0.01}$)(Figure 2.17 on page 46).

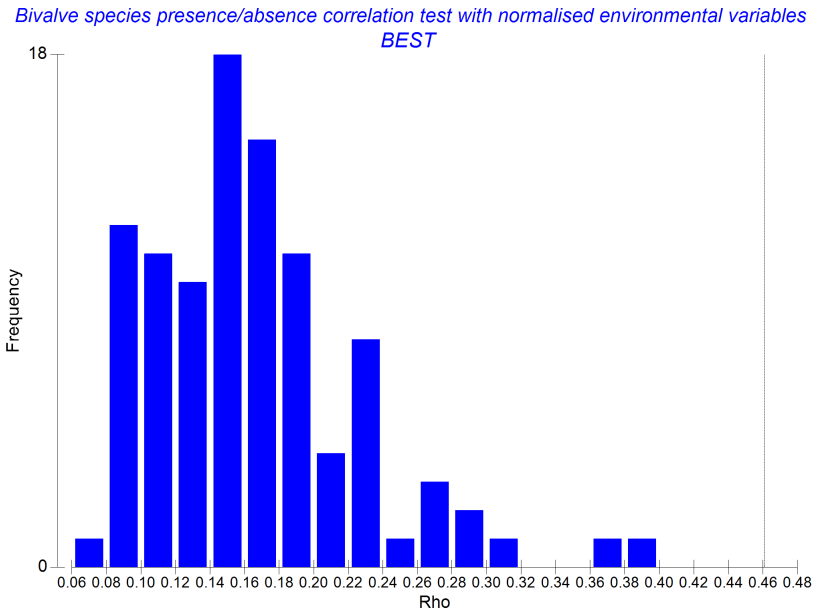
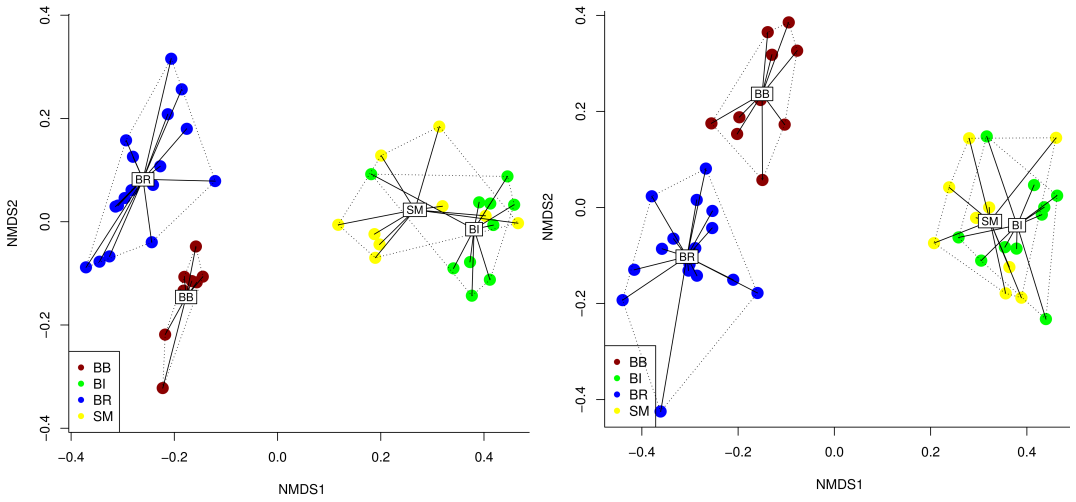


Figure 2.17. Test of Species Presence correlation with Environmental variables (Sediment type, Salinity, Organic content, RPD). The null hypothesis of the best correlation (light grey vertical line at 0.461) is compared to permuted correlations (blue). The null hypothesis of no correlation, or random correlations was rejected.

Non-metric multidimensional scaling plots of differences between stations clearly differentiate between sites, with some overlap between Sandymount and Bull Island. A similar picture emerges from analysis of bivalve abundances (Figure 2.18a) and biomass of all species (Figure 2.18b). Differences between the sites were formally tested using a permutational multivariate analysis of variance (PERMANOVA). Significant differences between the sites were noted in both abundance of bivalves (Pseudo-$F_{3,42}$=46, $\mathbf{p < 1e\text{-}4}$), and biomass of all species (Pseudo-$F_{3,42}$=33.4, $\mathbf{p < 1e\text{-}4}$). 10,000 random permutations were generated in order to compute a p value for the Pseudo-F statistic. The distribution of the Pseudo-F statistic for the permuted distance matrix indicates that is exceptionally unlikely that the observed differences between sites are due to chance effects. The assumption of homogeneity of multivariate dispersion among sites was tested using a PERMDISP analysis. The null hypothesis of equal dispersion in every group was rejected (**p=0.014**), however given the degree of difference between sites, the analysis would be robust to the observed small differences in dispersion.

SIMPER analyses, conducted to determine the species contributing most to the Bray-Curtis distance between stations at different sites, placed *M. tenuis* in the top two species for differentiating every pair of sites by bivalve abundance with the exception of Blackrock-



(a) Abundance of bivalves (b) All Biomass

Figure 2.18. Non-Metric Multidimensional Scaling plot of differences in bivalve abundances and biomass of all species among stations, fourth-root transformed. BB = Balbriggan, BI = Bull Island, SM = Sandymount, BR = Blackrock.

Balbriggan, where it was third. *Cerastoderma edule* was responsible for the greatest proportion of difference between sites in terms of all biomass.

2.3.4 Dominance and abundance/biomass comparisons

Cumulative abundance and biomass values respectively for the first n species are plotted against n for each n in 0 up to the number of species. The species present are ranked separately according to their proportion of overall biomass and abundance. Under undisturbed conditions it is expected that the biomass curve will be higher than the abundance curve. Comparisons of abundance and biomass for the four sampling sites used the W-statistic (Clarke, 1990), an index which maps the relative dominances of abundance and biomass to a value between -1 and +1, for which lower values indicate increasing levels of disturbance. W values were recorded as -0.06 for Blackrock (Figure 2.19), 0.165 for Sandymount (Figure 2.20), -0.057 for Bull Island (Figure 2.21) and 0.057 for Balbriggan (Figure 2.22).

Sandymount and Bull Island had the highest values for indices of bivalve diversity (H) (Shannon (1948), Table 2.3) and evenness (Pielou (1966), Table 2.4)

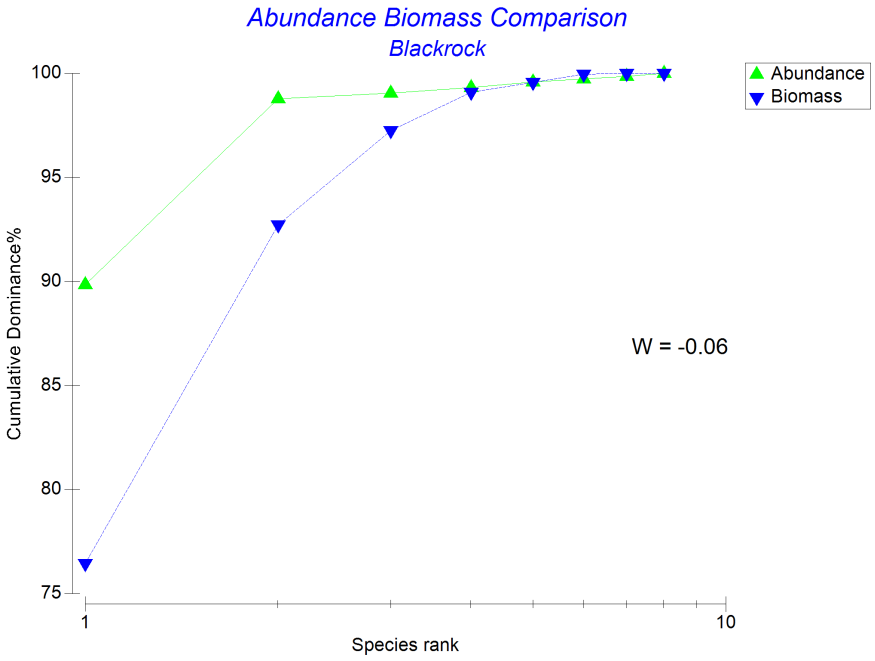


Figure 2.19. Abundance and Biomass curve for bivalve species in Blackrock, with W-statistic (the degree to which biomass dominance is greater) indicating moderate disturbance.

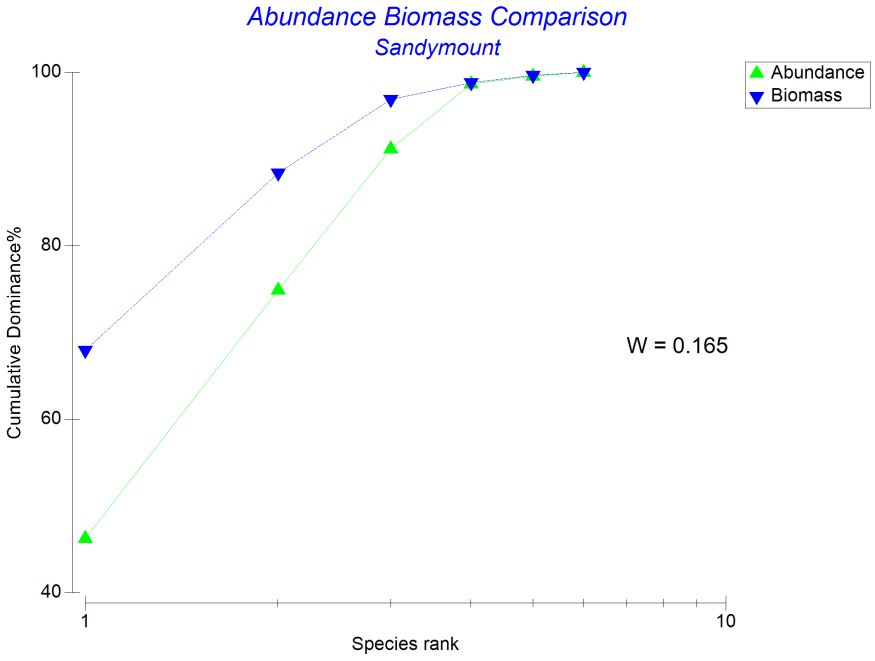


Figure 2.20. Abundance and Biomass curve for bivalve species in Sandymount, with W-statistic, the degree to which biomass dominance is greater, indicating low disturbance

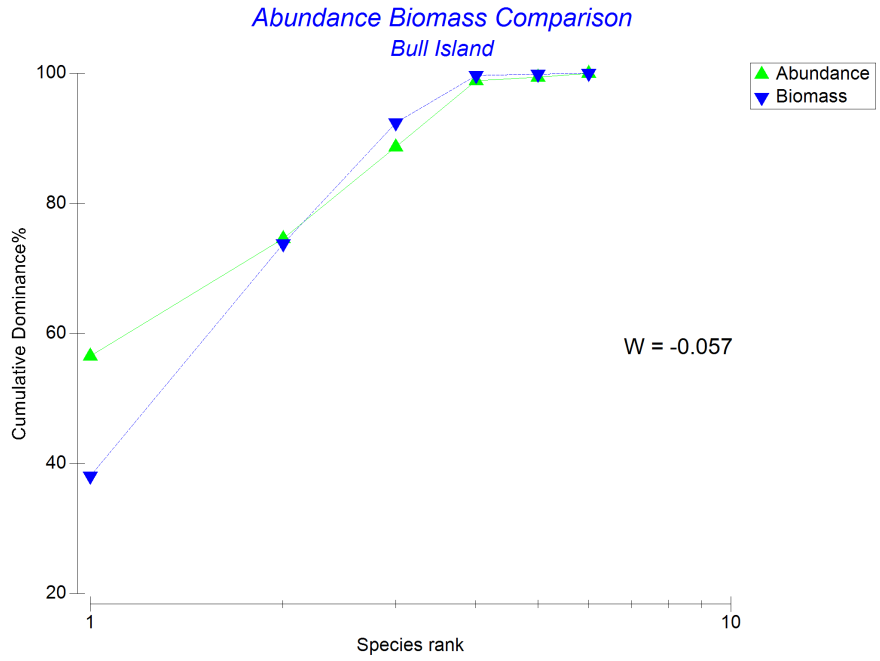


Figure 2.21. Abundance and Biomass curve for bivalve species in Bull Island, with W-statistic, the degree to which biomass dominance is greater, indicating moderate disturbance

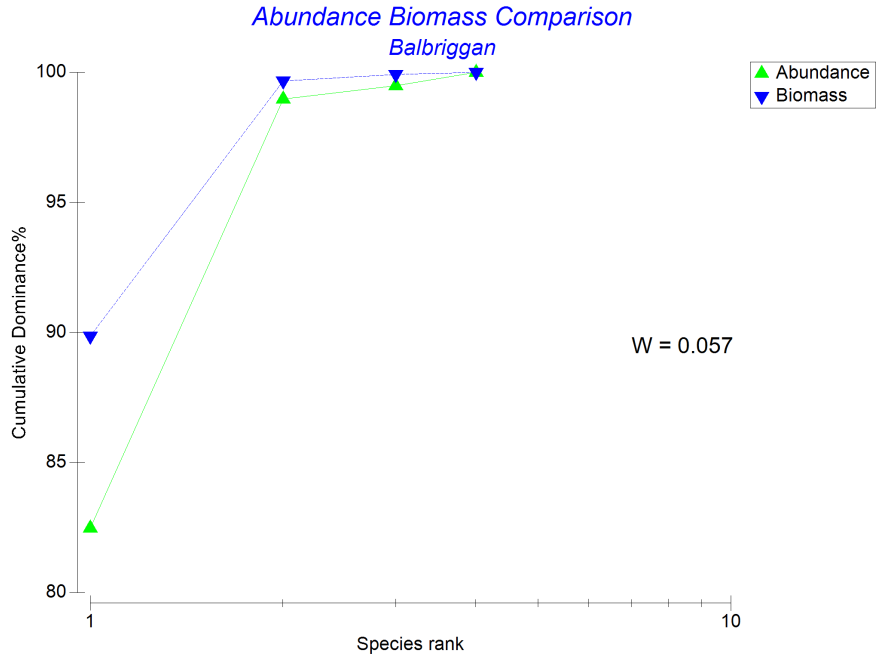


Figure 2.22. Abundance and Biomass curve for bivalve species in Balbriggan, with W-statistic, the degree to which biomass dominance is greater, indicating low disturbance

Table 2.3. Shannon's diversity indices (H) for the bivalves at four sites.

Site:	Shannon's Index of Diversity
Blackrock	0.38
Sandymount	1.27
Bull Island	1.19
Balbriggan	0.50

Table 2.4. Pielou's evenness indices for bivalves at the four sites.

Site:	Evenness
Blackrock	0.18
Sandymount	0.71
Bull Island	0.67
Balbriggan	0.36

2.3.5 Shell thickness and sediment type

Specimens collected for analysis and measured for length and shell thickness, exhibited a significant interaction between species and shell length and shell thickness (Table 2.5). The increase in shell thickness with length was greatest for *L. balthica*, increasing over 0.1 mm per mm increase in length, while *F. fabula* had the thinnest shells and also the smallest increase in thickness with length. *S. plana* and *M. tenuis* also had small increases with increased length, at under 1 %. An individual of a standard 15 mm shell length of *L. balthica* has a 0.57 mm thick shell, while such a standard individual of *D. vittatus* has a 0.26 mm thick shell. *S. plana* and *M. tenuis* have 0.16 mm thick shells in standard 15 mm individuals, while a standard *F. fabula* has a shell only 0.11 mm thick.

Table 2.5. Shell thickness in relation to length and species. Intercepts spX (where x is the name of a species) and slopes length:spX for each species are defined with reference to the intercept for *L. balthica* (Intercept) and the slope (length coefficient) for *L. balthica* (length)

	Estimate	Std. Error	t value	$Pr(>\|t\|)$
(Intercept)	-0.98	0.104	-9.479	**2.59e-15**
length	0.1	0.006	15.91	**<2e-16**
spfabula	0.99	0.17	5.84	**7.72e-08**
spplana	1.02	0.12	8.27	**9.03e-13**
sptenuis	1	0.19	5.31	**7.49e-07**
spvittatus	0.85	0.34	2.54	**0.01**
length:spfabula	-0.096	0.014	-7.05	**3.17e-10**
length:spplana	-0.095	0.007	-13.93	**<2e-16**
length:sptenuis	-0.094	0.014	-6.81	**9.49e-10**
length:spvittatus	-0.078	0.016	-4.81	**5.81e-06**

Sediments found at these characteristic stations had differing compositions, in terms of gravel, sand and silt/mud consistency (Table 2.6).

Table 2.6. Sediment composition at the sites where specimens for shell thickness analysis were collected. Gravel (particles $> 2mm$), Sand (2 mm$>$ particles $>$ 0.063 mm) Silt/mud (particles $<$63 μm) (Folk, 1954).

Species:	Gravel	Sand	Silt
D. vittatus	0.46	97.25	2.28
M. tenuis	0.34	96.47	3.19
F. fabula	0.10	97.66	2.23
S. plana	0.01	91.78	8.21
L. balthica	0.14	92.91	6.94

M. tenuis was also found at or near all of these typical locations, while *D. vittatus* or *F. fabula* were not found in any samples in which *S. plana* or *L. balthica* were present. This may be owing to a preference for muddy sediment by *S. plana* and *L. balthica*, more suited to deposit feeding, and an avoidance of muddy sediments by *F. fabula* and *D. vittatus* in particular as a suspension feeder.

2.4 Discussion

It must be noted that this field distribution investigation deliberately targeted known areas of Tellinoid presence, although overall abundance estimates match previous investigation of the bay (Wilson, 1982b). Transect analysis revealed a close association of *F. fabula* with consistent immersion (including in depressions or channels on the beach). This is a refinement to the previously held view of *F. fabula* as being found at or below the low water mark only. Two distinct biotopes were found to exist in the Dublin Bay littoral zone from the transects selected, distinguished by silt, redox potential discontinuity depth, salinity, and the biota found therein. Each species dominated, or was most common in one or two sites, with corresponding environmental conditions (Table 2.1). Some species cannot be differentiated based on these environmental criteria alone, for example, *S. plana* and *L. balthica* both prefer silty sediments with a shallow oxygenated layer, in contrast to *D. vittatus* and *M. tenuis*, which dominate where sand is clean rather than silty, with the anoxic layer at a greater depth than the sampled 20 cm. Silt is the most distinctive difference between the biotopes. Salinity was low at the respective sites where *S. plana* and *L. balthica* were most abundant, but was high at other stations where *L. balthica* and *S. plana* were found, so appears to be not so much a determining but rather incidental characteristic in this respect. While high salinity is not a limiting factor for *L. balthica*, low salinity may give *L. balthica* a potential competitive advantage, as it is exceptionally tolerant of brackish conditions, as demonstrated by its high abundance in the Baltic sea (Jansen *et al.*, 2009). The oxygenated sediment layer was shallower where *F. fabula* was the most abundant Tellinoid, than where *M. tenuis* or *D. vittatus* were more common. The oxygenated layer was extremely shallow where *S. plana* and *L. balthica* were found.

In terms of species abundance there is a gradual shift from *F. fabula* to *M. tenuis* from below the low water spring mark to the high water mark in Blackrock. This observation does not agree with previous descriptions of distribution indicating that the two populations are distinct apart from some overlap occurring at spring low water mark (Wilson, 1978, 1976b, 1981; Stephen, 1928).

Based on the continuous colonisation by *M. tenuis* to below the low water mark, both in Blackrock and Balbriggan, but the decreased numbers of *M. tenuis* below the low water mark in Blackrock only, it would appear that *M. tenuis* is better adapted than *F. fabula* to the environment above the low water mark, but is less suited than *F. fabula* to conditions below low water. *M. tenuis* was found to be the most abundant bivalve, being found at all

sites, and in some stations being found at abundances of over 1000 m^{-2} or infrequently (only one individual was found in a cumulative 0.8 m^2 sampled at Bull Island). This suggests that while *M. tenuis* is the most generalist in terms of resource partitioning and niche division, it is less suited to the environment at Bull Island. Reasons could potentially include potential competition with *L. balthica* and *S. plana*, predation, disease or inability to tolerate fine sediment (mud). Its presence in all sites evidences the fact that it can tolerate a broad range of environment and sediment types, but the difference in abundance suggests that it prefers less silty/muddy habitats, which is as expected for a primarily suspension-feeding Tellinoid (Wilson, 1990).

The other four species constitute two mutually exclusive groups. No *S. plana* or *L. balthica* were found at the same station as *D. vittatus* or *F. fabula*, or indeed at the same site as one another. *S. plana* and *L. balthica* were absent from Blackrock and Balbriggan, while *D. vittatus* and *F. fabula* were absent from Sandymount and Bull Island. *S. plana* and *L. balthica* are sympatric, varying in respective dominance of site within the muddier stations, while *D. vittatus* and *F. fabula* are almost allopatric, with only two individuals of *D. vittatus* being found in stations within the range of, but not dominated by *F. fabula*. Unlike the results of this investigation, *F. fabula* are often found in finer sediments than their sympatric relative *M. tenuis*, thought to be excluded by inadequate capacity to deal with large quantities of fine particles (Wilson, 1990). The large number of influencing and possibly interacting factors relative to the number of data points limits the extrapolation of statistical predictive rules, which hold for all sites, owing to potential over-fitting (Hylleberg and Riis-Vestergaard, 1984). Populations of *F. fabula* and *M. tenuis* were thought previously to display dramatic shifts at the mean low water mark (Wilson, 1988; Stephen, 1928), rather than the gradual reduction in abundance and eventual absence and elimination of *F. fabula* found in this study as one moves inshore from the low water mark.

As in Wilson (1982b), bivalves still dominate the standing biomass. In this investigation *M. tenuis* was the most abundant bivalve, followed by *S. plana*, in contrast to previously where *Cerastoderma edule* was the most abundant (Wilson, 1982a). Biomass is still dominated by *Cerastoderma edule* with over 40 % of total biomass. *S. plana* constituted 20 % of biomass, *Mya arenaria* made up 9 %, and *M. tenuis* had the fourth highest biomass, at 6 %. *M. tenuis* were found at found at 63 % of stations in the bay and all stations in Blackrock. The abundance of *M. tenuis* remains particularly high in Blackrock. There were a limited number of *M. tenuis* west of Bull Island, which had not previously been recorded.

M. tenuis had been effectively absent from the range of *L. balthica* on the North side of the bay, but co-occurred to a reasonable degree on the South side. *M. tenuis* was however less abundant where *L. balthica* was present on the South side (Wilson, 1982a). The general pattern is repeated in this study, with no more than a single *M. tenuis* at any station on the North side of the bay containing *L. balthica*, with a greater degree of co-occurrence on the South side, but still much reduced abundances of *M. tenuis* where *L. balthica* were found.

As in the previous 1977 survey, *F. fabula* still frequently co-occur with *M. tenuis*, but not in the stations where *M. tenuis* were most abundant. *F. fabula* was found only in Blackrock. Similarly, *F. fabula* were again considerably more abundant near the LWM close to Blackrock. Previously, small numbers of isolated individuals of *D. vittatus* were noted, all on the South side of the bay, with low numbers of *D. vittatus* scattered close to the LWM; here, only two individuals of *D. vittatus* were found in the bay. *D. vittatus* were found at high abundances in Balbriggan. In 1977, isolated individuals of both *F. fabula* and *D. vittatus* were found near the LWM (Wilson, 1982a), however only two individuals of *D. vittatus* were found here, both towards the upper reaches of the range of *F. fabula*.

L. balthica was found behind Bull Island and on Sandymount strand, its overall distribution similar to 1977 although somewhat reduced in range, with abundances remaining particularly high in the shelter of Bull island. The distribution of *S. plana* was again similar to *L. balthica*, however, while *S. plana* still frequently coincides with *L. balthica*, it previously only occurred in five stations without *L. balthica*, which then had a much greater range (Wilson, 1982a). This co-occurrence did not feature as strongly in this investigation, with *S. plana* found without *L. balthica* in half of the stations where it occurred. The range of *L. balthica* has decreased since 1977.

Shannon Index (H) values for bivalves ranged from 0.38-1.27 in this investigation. Blackrock, with a H value of 0.38, and Balbriggan, with a H value of 0.5, were the sites containing the greatest abundances of suspensivores. Sandymount (1.27) and Bull Island (1.19) contained greater abundances of deposivores. As diversity indices are sensitive to the sampling quantity, the difference between H values is of greatest interest. Diversity and Evenness of bivalves were far higher in Sandymount and Bull Island, where deposivores are abundant, than in Balbriggan or Blackrock, where suspensivores dominate. The specialisation of deposivores to occupy several niches, and lack of niche division among suspensivores, implies that evenness should be higher in deposivore communities (Levinton, 1972). The results of this study support greater evenness among deposivores.

Chapter 3

Functional Morphology and Allometric Relationships of the Labial Palps and Gills of Tellinoids from Dublin Bay

Abstract

Suspension and deposit-feeders are important members of estuarine ecosystems, recycling pelagic and benthic nutrients, respectively. Differentiating between these groups gives a better understanding of nutrient cycling pathways and trophic transfers in marine systems. The palp area to gill area ratio (P:G) is indicative of feeding type where a high ratio signifies deposit feeding and a low ratio indicates suspensivory. The gills and palps of five species of Tellinoids (Blainville, 1814) were examined (*S. plana*, *M. tenuis*, *L. balthica*, *F. fabula*, *D. vittatus*) using the P:G ratio to classify their mode of feeding. The average P:G ratios found were as follows: *L. balthica*: 4.12; *S. plana*; 1.38, *T. fabula*; 1.31, *M. tenuis*; 0.78, *D. vittatus*; 0.5. There was a larger difference between P:G of *L. balthica* and *S. plana* than expected. The novel photographic analysis technique used, was a successful way to compare the area of gills and palps. Allometric growth of palps and gills relative to length and to each other were examined in order to determine whether feeding mode changes with growth. No conclusive change in feeding mode with dry flesh weight or shell length was seen.

3.1 Introduction

3.1.1 Gills and palps

The gills and palps of bivalves are important feeding organs. Cilia on the gill surface generate feeding currents, which draw particles of food through the inhalent siphon and on to the palps. Cilia on the palps act to manipulate and sort the captured particles for ingestion, which occurs when material, having been drawn through the inhalent siphon is captured and sorted, and enters the mouth. Gills are also used for bivalve respiration, drawing in oxygenated water and facilitating gas exchange. Suspensivores have larger gills than palps for pumping water, whereas deposivores have relatively larger palps than gills for sorting material (Compton *et al.*, 2008). The ratio of gill area to palp area (Wilson, 1990), gill mass to palp mass (Compton *et al.*, 2007), or the ratio of palp area to gill area (Payne *et al.*, 1995) can be used, with the latter chosen in this investigation. Gills must possess the area required for adequate gas exchange, although the eulamellibranchia have larger gills than the protobranchia with similar metabolic requirements (Wilson, 1981). The other function of the gill is the generation of an inhalent current for drawing in food particles, which is also linked to metabolic requirements. The pumping rate of bivalve gills is proportional to the gill area (Hughes, 1969). The area of the palps is indicative of the sorting effort required. The palp area is therefore the metric which changes most with feeding behaviour, and the gill area is the reference point against which this is measured. Ecophenotypic variation of palp and gill size within bivalve species has been noted to include greater variation in palp sizes, after shell length is taken into account. Most allometric variability in gill size is owing to exposure, but palp size is also affected by sediment grain size and density (Rullens, 2016). The palp size of a bivalve is a proxy for the importance of the palp's function. Proportionally larger palps tend to indicate that a species is a deposit feeder, as it must expend more effort sorting food from unsuitable, ingested detritus (Compton *et al.*, 2008). A difference in the palp to gill area ratio (P:G) between species may imply different feeding habits and in turn influence the understanding of species distribution and community composition (Wilson, 1990). It has previously been found that there is no simple or abrupt division between suspension-feeders and deposit-feeders, but rather that they form a continuum (Wilson, 1990), although *D. vittatus*, with siphons shorter than typical suspensivores, is assumed to be an obligate suspensivore (Riisgård and Kamermans, 2001), while other bivalves, such as the protobranch *Nucula turgida*, possessing a primitive gill used almost exclusively for respiration, is an obligate deposivore (Wilson, 1981).

3.1.2 Rationale for the use of P:G ratio

The principle of using the P:G for classification of bivalves is based on the contrasting and complementary functions of these organs. In general, suspensivores need large gills to pump large quantities of seawater and deposivores need large palps to sort large amounts of sediment. P:G and G:P ratios have both been used in other researchers' previous work. Having found no explicit justification for either format, and considering that one is the inverse of the other, P:G ratio was used as a descriptor for the following reason: Gill area has a lower bound determined by the metabolic requirements of the animal and is influenced by factors outside the scope of bivalve feeding mode, *i.e. D. vittatus* as an active animal naturally has large gills to provide oxygen for its high metabolism. The oxygen consumption of a 30 mg (DFW) specimen of *D. vittatus* has been estimated at up to 20 $\mu g \cdot h^{-1}$ (Ansell, 1973), while that of a 15 mg specimen of *M. tenuis* has been estimated as 6 $\mu g \cdot h^{-1}$ (Trevallion, 1971). The high metabolism of *D. vittatus* has resulted in apparent epidemic mortality of *D. vittatus* during periods of restricted food availability, owing to metabolic stress (Ansell and Sivadas, 1973). While some protobranch bivalves such as *Nucula turgida* have comparable oxygen consumption to eulamellibranchs with much larger gills, this appears to come at the cost of a diminished ability to oxyregulate, while eulamellibranch bivalves may switch their gill behaviour for increased oxygen uptake rather than food gathering (Wilson and Davis, 1984). Palp area is determined by a combination of factors including the volume of material to be sorted and the food concentration in the ingested material that the species and animal typically encounters. Palp area is therefore directly related to feeding mode and by describing the ratio in its terms, emphasis is placed on palp area as the salient characteristic.

3.1.3 Gill function

Within the bivalve, hydromechanical and mucociliary actions move particles over the gills. Lateral cilia on the gill filaments move and maintain the flow of water through the mantle cavity and the gills for respiration and feeding. The water is subsequently strained at the entrance to the inter-filament spaces by the latero-frontal cilia. These particles are then cast onto the frontal surface of the gill filaments (Gosling, 2008). These filaments are covered with mucocytes, where the particles are trapped in a fine mucus layer overlying the frontal cilia. The particles are transported towards ventral (marginal) ciliated particle (food) grooves (Beninger *et al.*, 1997). The exact mechanisms of particle capture are controversial (Ward *et al.*, 1998, 2000; Riisgård and Larsen, 2000; Ward and Shumway, 2004), but it is under-

stood that particles are captured as they encounter the frontal surfaces of the gill filaments. The material is combined into mucus strings that are transported along the grooves towards the labial palps. The gills themselves, once thought of as mere automated sieves, are able to control the rate at which suspended material is taken from the surrounding water. Gills control the rate by altering the angle of ciliary beat or muscular expansion of the ostia. The latero-frontal cilia themselves may act as solid paddles moving particles along (Ward *et al.*, 1998). At high particle concentration mucus strings from the ventral food grooves may not enter the palps at all but may be rejected at the gill-palp junction as pseudofaeces. Eumellibranchs carry captured particles on the gill to the labial palps, but are capable of closing the ventral gill particle groove after prolonged exposure to particles, essentially shutting down the feeding function of the gill (Beninger *et al.*, 1997; Gosling, 2008). The water then flows to the suprebranchial cavity and out of the exhalent siphon, particles having been captured by the gill (Ward and Shumway, 2004). Gills are involved in gas exchange, part of the oxygen demand of the animal is provided by the gills, with the mantle providing most of the remaining respiratory capacity (Eble and Scro, 1996). In filter feeding the ciliation of gills probably constituted adaptation for respiration and cleaning of the gill (Jorgensen, 1990). It was then later co-opted for the transport of potential food particles to the mouth, this is an example of ex-adaptation. It was first suggested by Yonge (1949) that habitat and the characteristic of the material carried in the inhalent current is what controls the form of the gill and the nature of its currents.

3.1.4 Palp function

In bivalves the palps are a particle selection and sorting site. Particles are moved along the ciliated ventral particle grooves in a mucus string on the gill to the gill-palp junction. The palps are located on either side of the mouth. The palp outer surface is smooth and connected to the inner surface with muscular connective tissue. The inner surface is folded into ridges that have various ciliary tracts. When the mucus string reaches the palps it detaches from the gill onto the ridged inner surface of the palps. Material for ingestion passes over the palp crests at right angles to the ridges. While it is passing over the crests it is subject to the apposition and grinding motion of both palps. The cord is destroyed and the material in the oral region is then in the form of a mucus slurry (Ward *et al.*, 1994; Beninger *et al.*, 1995). The particles released from the mucus strings together with those from the dorsal grooves are sorted on the palp ridges and then either enter the oral groove or are rejected off the palp.

Rejection of material is more likely when small palps have large volumes of material to sort. After prolonged feeding, mucus particle cords from the gill can be transported obliquely over the palp crest to the ventral region of the palp for rejection as pseudofaeces.

Actual particle selection on the eulamellibranch labial palps has not been described in detail. A good understanding of the pseudolamellibranch was, however, completed; the process in eulamellibranchs is similar. The process is described in pseudolamellibranchs in accordance with Ward *et al.* (1994): particles in the gills are transported in the dorsal and ventral grooves towards the labial palps. Particles in the dorsal tracts are transported in a slurry towards the gill-palp junction. They leave the junction by one of four routes: 1) into the oral groove on the palp and on to the mouth; 2) onto the ridged sorting surface of the palp; 3) onto the smooth ciliated tract of the palp edge; or 4) onto the anterior margin of each demibranch for posterior transport. The cilia on the palp ridges have different functional roles: rejection tracts that transport particles to the palp margins; oral acceptance tracts which move particles to the mouth; and re-sorting tracts that either accept or reject particles. The route taken is determined by ambient particle concentration. If ambient concentration of particles is high, rejection off the palp edge results in pseudofaeces production (Ward *et al.*, 1994).

In eulamellibranchs the labial palps are the main site of ingestion volume control, with the lips acting as an additional site. It has been suggested that particle sorting and selection on the labial palps is a rate-limiting step of pre-ingestive feeding processes in bivalves and that interspecific differences in particle handling on the labial palps may be owing to palp morphology and function (Dutertre *et al.*, 2009).

3.1.5 Functional relationships of palps and gills

There is a general tendency for palps to be larger in mud-living species, and for mud-dwelling individuals of a species to have larger palps and smaller gills than sand-dwelling individuals of the same species (Ward and Shumway, 2004). In some species, the total tissue mass between gill and palp has a strong correlation with body mass, while P:G ratio varies considerably, therefore there is an inverse relationship of P:G (Honkoop *et al.*, 2003). The relationship between area of palps and gills suggests that where gills are large they are capable of considerable selection before material is passed to the palps, or that little selection effort is required, but where larger volumes of material must be processed the palps have the task of selection before food enters the mouth. In *D. vittatus*, small palps may be correlated with an absence of fine material, i.e. a muddy substratum correlates with larger palps. The principal mor-

phological difference between the Tellinids *F. fabula* and *M. tenuis*, is the higher P:G ratio of *F. fabula* than *M. tenuis*, which is an adaptation to a more deposit-feeding mode in *F. fabula* (Wilson, 1990). Smaller gills in *L. balthica* may be owing to the greater ease at which fine particles from a mud stratum are drawn in. Essentially, an animal that has a requirement to sort large amounts of material, deposit feeds, and has larger palps (Yonge, 1949; Wilson, 1990).

To determine whether diet is related to the relative area of gills and palps in bivalves, carbon and nitrogen stable isotope signatures have been compared with the stable isotope signatures of available sources of suspended material and of the sediment (Compton *et al.*, 2008). Isotopic signatures are combinations of ratios of non radiogenic isotopes of elements in a sample, for example ${N_7}^{15}$ and ${C_6}^{13}$ (Maberly *et al.*, 1992). The degree to which isotope signatures indicate suspensivory is strongly correlated with the gill:palp mass ratio of each bivalve species. The data pointed to a continuum of behaviours in terms of resource usage, with feeding mode related to the relative masses of gills and palps. P:G ratios were inferred from Compton *et al.*'s (2007) gill/palp mass ratios (Appendix A.1). *S. plana* had a P:G ratio 1.38 times that of *M. tenuis*, while *L. balthica* had a ratio 1.48 times that of *M. tenuis*, and 1.07 times the ratio of *S. plana* (Compton *et al.*, 2007).

3.1.6 Allometric growth in bivalves

The difference in the area of the gills and palps in bivalves with the same body plan can be explained by allometric growth, where the growth rates of parts of the organism differ from the growth rate of the organism (Snell, 1892; Huxley and Callow, 1933). Isometric growth predicts that all the body parts grow at approximately the same rate, and that adult proportions are not different from those of the juveniles. Whereas allometry predicts that these body parts grow at different rates, and can differ between adult and juvenile forms, isometry predicts that the relationships between shell length and weights should have an exponent of 3.0. (Equation 3.1). (In the following equations k is an arbitrary constant representing proportionality).

$$mass = k * length^3 \tag{3.1}$$

The allometric relationship of food intake (metabolic rate) to mass has been found to yield a mass exponent of approximately 0.67 (Equation 3.2 (Calow, 1981)). The mass exponent for oxygen consumption for 16 bivalve species in Scotland was recorded as 0.7 (Ansell, 1973),

which accords with the figure of 0.67.

$$metabolic\ rate = k * mass^{\frac{2}{3}} \tag{3.2}$$

As gill and palp area are connected to the food gathering potential (to support metabolic rate), a weight exponent of 0.67 is expected, equivalent to a length exponent of 2.0. This connection is a proportional relationship such that the surface area of the organ determines its efficacy. In the absence of other factors, gills and palps are, therefore, expected to grow isometrically, as the area of each organ determines the food gathering potential of the animal (Equation 3.3).

$$area = k * length^2 \tag{3.3}$$

Allometric (i.e. non-isometric) growth may indicate a change of feeding strategy with size. This is quantified by determining the relationship between growth of the organism and growth of the part in question, log transforming the value, and testing the difference between the measured slope and that predicted by isometry. In the case of area-based quantities compared to linear measurements of organism size, the expected slope is 2.

3.1.6.1 Palp area to gill area ratio

Areas of organs scale isometrically with the square of length, while volumes or masses scale isometrically with cube of length. Any scaling of area to mass with an exponent other than $\frac{2}{3}$ of mass is therefore allometric growth, and may provide clues regarding the optimal sizes of organisms. Efficiency of gills and palps is related to surface area of these organs. With respect to oxygen requirements, area is therefore an important characteristic of gill function. It is therefore appropriate to determine gill and palp sizes in terms of area. Allometric growth is of interest because it suggests that either the resource requirements are scaling differently to the expected exponent of $\frac{2}{3}$ (Calow, 1981) or its food intake capacity is scaling at a different rate to typical metabolic requirements.

3.1.7 P:G ratio and niche determination

Niche, as defined by Warwick (1982), is a multidimensional space covering possible values for factors, such as food availability and type, temperature, substratum amongst others. Niche width refers to the range of values which are acceptable for a given species. Warwick (1982) hypothesised that this is unspecialised, *i.e.* broad, for suspensivores and specialised/narrow for deposivores. Suspensivores capture pelagic algae and suspended detritus from the surrounding sea water and live wherever they can burrow or anchor. A higher P:G is indicative

of deposit feeding. As palps are used for sorting, a bivalve species may have evolved bigger palps in an area with high inorganic particle content in the seawater-sediment interface, as the inorganic material would need to be separated from the useful food. Pelagic plankton is more likely to be eaten by suspensivores, while deposivores can eat detritus and bottom dwelling algae. Another potential view of niche width is that P:G is itself a dimension of niche, and therefore species with high variation in P:G among individuals of the same species occupy a broader niche.

Knowing where species appear on the deposit or suspension feeding array in Dublin Bay gives a better understanding of how they are likely to interact with one another, directly or indirectly. Suspension feeders do not tend to interact directly with other organisms, however when occurring in large densities they may deplete the food supply for other organisms, including, to an extent, deposit feeders.

3.1.8 Aims

The identification of deposit or suspension feeding, according to P:G ratio, for the five species of Tellinoids in Dublin Bay was the primary element of this investigation. The established correlation between P:G and feeding mode, together with the determination of whether growth of the palps and gills is isometric, provides a more detailed characterisation of the feeding capabilities, and the degree to which feeding mode changes with size.

H_1 The Littoral Tellinoid species of Dublin Bay have P:G ratios whose arrangement in descending order agrees with their classification from deposivore to suspensivore.

Classifications were constructed from the literature, including some which referred to orderings based on ratios (Wilson, 1990; Compton *et al.*, 2008). It was expected that *D. vittatus*, as an obligate suspensivore, would have a lower P:G ratio than the other Tellinoids.

H_2 There was no change in feeding mode with shell length or DFW of any Tellinoid species examined, *i.e.* all relationships between gill area, palp area and DFW or length are isometric.

Any such change would indicate a change in strategy for the organism, and it would have to be studied separately at different life stages, as extrapolation of results from before/after the switch would be invalid. To test this hypothesis, the relationship between the dry flesh weight (DFW) and total shell length, and the area of the gills and palps, was determined and the results tested to determine whether such relationships deviate from isometric growth.

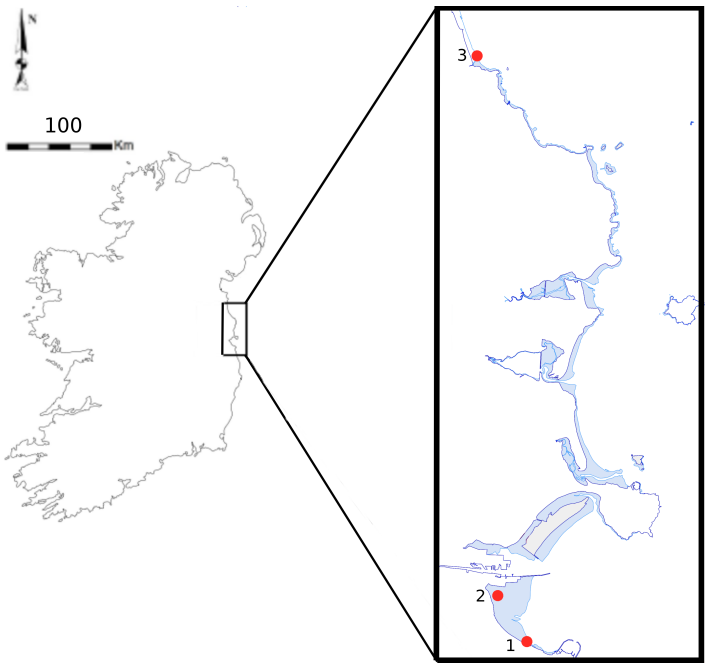


Figure 3.1. Map of Ireland showing the location of the sampling area, with expansion showing sampling locations labelled with red dots: 1: Blackrock, 2: Sandymount, 3: Balbriggan. Map credit Google maps (2017).

3.2 Methods

Five species of Tellinoid bivalves were collected from locations in Dublin Bay and in Gormanstown Beach, Balbriggan during September 2012, taken from areas known to contain populations of Tellinoids (Wilson, 1982b, Wilson pers. comm). *F. fabula* and *M. tenuis* were collected from Blackrock, Dublin Bay (53°30'33.0" N, 6°17'59.5" W). *S. plana* and *L. balthica* were collected from Sandymount, Dublin Bay (53°32'76.7" N, 6°19'64.8" W) and *D. vittatus* was collected from Balbriggan, North County Dublin (53°63'60.4" N, 6°20'80.2" W) (Figure 3.1). A spade was used to take a sample of the sediment which was subsequently placed in a 1 mm sieve. The sieve was shaken in sea water to separate the sediment from any bivalves present. Bivalves were then removed and transported to the laboratory, in a bucket containing sediment and water from the collection site.

Healthy specimens of each species were chosen for further examination, endeavouring to cover the complete range from the largest to the smallest specimens sampled, without leaving inordinately large gaps in size range. The wet weight of each individual was recorded to ±0.01 mg using a calibrated Mettler Toledo B154-S analytical balance after blotting the animal on tissue paper. Measurements were recorded to ± 0.01 mm. Shell length (mm), shell

depth (mm) and shell width (mm) were recorded with a Vernier callipers to 0.01 mm for each individual after the experiment had been completed to minimise animal disturbance/handling prior to the experiment. Animals were dissected from their shell and dry weight (mg) was established for shell and flesh separately by drying in an oven at $105 \pm 5\,^{\circ}\mathrm{C}$ for 24 hours and weighing. The resultant measure for the flesh is referred to as dry flesh weight (DFW) (mg). The samples were then placed in a furnace at 450 °C for 6 hours in order to determine loss on ignition and organic matter content and thus ash free dry weight (mg) (Velasco *et al.*, 2006). DFW, also known as shell-free dry weight (SFDW) has all the advantages of ash free dry weight (AFDW), typically having a value approximately equal to $1.2 * AFDW$ (Ricciardi and Bourget, 1998). Difficulties have previously been noted in determination of AFDW for small specimens (Widbom, 1984), possibly owing to the oxidative weight gain (Piehl, 1974) of aluminium foil and dishes typically used in the procedure (Mann and Gallager, 1985). While DFW is generally considered to be an underestimate, owing to loss of volatiles in drying (Ivell, 1983), the loss is typically proportional to DFW, and the error is also present in AFDW computations. For these reasons, and because DFW values were more reliable for the quantities processed in this work, and DFW was selected as the primary mass-based metric.

Subsequent experimental procedure followed that of Wilson (1990). Specimens were narcotised to avoid the contraction of tissues by gradually adding 7% MgCl (the most effective narcotising agent (Suquet *et al.*, 2009)) solution in seawater to the holding chamber and subsequently holding in pure 7% MgCl for 30 minutes (Geiger *et al.*, 2007). The two valves of each bivalve were separated by cutting the left anterior adductor muscle with a scalpel (SS-10) and the animal was dissected out under a dissection microscope (Olympus SZ 40) with an AmScope 150W fibre optic, dual goose-neck, microscope light. The mantle was gently removed and the gill and palps were unfolded. The mantle cavity was flooded with 7% MgCl in seawater and the organs floated off the visceral mass (Hughes, 1969; Worrall *et al.*, 1983), so that their full area could be photographed. It was assumed that the left and right gill and palp were the same area, as confirmed by Wilson (1990) for two species; *M. tenuis* and *F. fabula*. As there was no difference between the right and left gill area or the right and left palp area, the less damaged was used. The experimental individual was placed on 1 mm^2 graph paper for scale and photographed (Figure 3.2). This calibrated image was used to calculate the surface area of the gills and palps respectively.

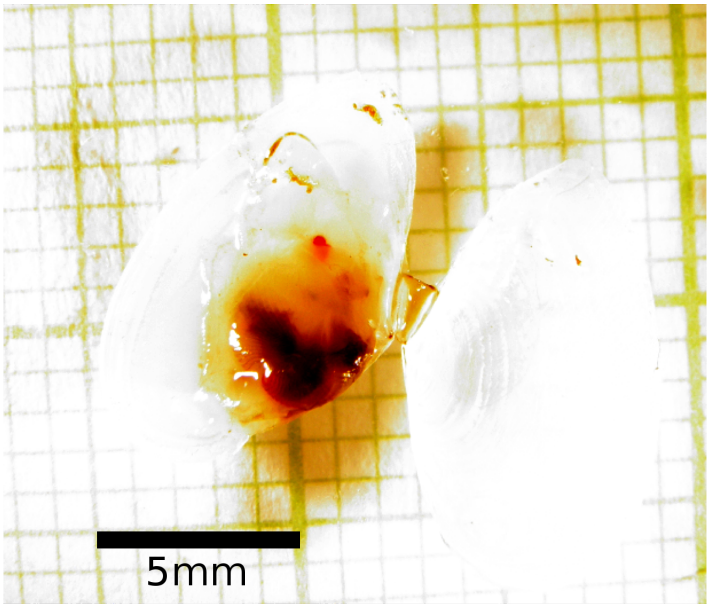


Figure 3.2. Dissected Bivalve: *M. tenuis* with open valves

3.2.1 Photographic analysis

Individual photographs were analysed using imagery software GiMP 2.8.3 (GNU Image Manipulation Program). Lines were drawn manually around a reference square (from underlying graph paper), and the palps and the gills using a polygon tool (the polygon tool allows selection and manipulation of an area). The function "color-extract" colour planes of red, green and blue (rbg), (Figure 3.3) was enabled in the software and the organs (gill and palp) were then overlaid with pixels of a separate pigment. These pixels were counted and compared to the pixels contained in the 1 mm square. The area provided by the software was in pixels and was later converted into mm^2 (Equation 3.4).

$$Organ\ area(mm^2) = \frac{Area\ of\ organ\ pixels}{Area\ of\ 1mm^2\ pixels} \tag{3.4}$$

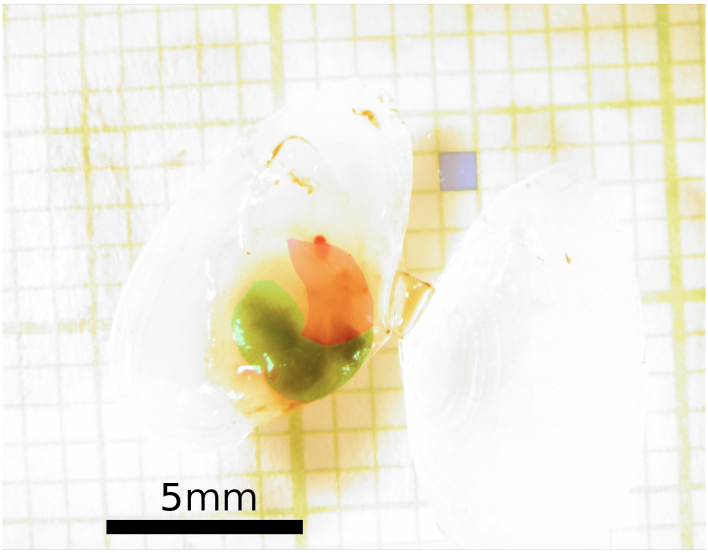


Figure 3.3. A photograph of a dissected bivalve used to determine the area of gills (green) and palps (red). The organs were outlined by eye using the GiMP polygon tool. A single square from a sheet of graph paper ($1mm \cdot 1mm$) was used as a reference, which was placed under the dissected bivalve on the photo, this was filled with pixels of pigment (shown in blue). The shading opacity was increased to 100%, giving solid colours within the polygons, which were then quantified by the software GiMP by counting the pixels of each solid colour.

3.2.2 Statistical methods

Data were recorded in Microsoft Excel 2008 for Mac (version 12.0), collated, exported in .csv format and subsequently analysed using the statistical package R (3.1.0) (R Core Team, 2016). The functional association of palps and gills was expressed as the ratio of P:G area. 17-21 individuals of each species were measured, and an effort was made to have individuals from a range of sizes, but this was not possible for *D. vittatus*, which therefore, despite being the second longest species, has the shortest range of lengths. The two largest specimens of *L. balthica* had a notably higher depth to length ratios, but otherwise there were no notable outliers. Initial examination of the data was carried out using scatter-plots and box plots. Data were log-transformed to allow the graphical comparison across different scales, and also to allow the determination of allometric growth coefficients. Allometric coefficients were determined by the slope of a fitted line in a linear regression of the log-transformed data. Regressions of palp area, gill area and P:G against DFW and total shell length were carried out in R.

3.3 Results

Summary results for the species investigated including mean length (mm), length range (mm) and mean P:G for each species, are presented alongside accepted feeding modes from the literature (Table 3.1). *L. balthica* had the highest P:G, while *D. vittatus* had the lowest P:G.

Table 3.1. Summary results for shell length and P:G for all species examined. The results include the mean (mm), range (mm), P:G and the currently accepted feeding mode from the literature for each species.

Species	N	Shell Length (mm)			Feeding Mode
		Mean	Range	P:G	(From Literature)
D. vittatus	19	21.58	19.06-24.18	0.5	Suspension (Yonge, 1949)
M. tenuis	17	12.8	8.95-15.76	0.78	Suspension/Deposit (Trevallion, 1971)
F. fabula	21	11	6.53-13.92	1.31	Suspension/Deposit (Wilson, 1990)
S. plana	18	31.95	13.54-46.82	1.38	Deposit (Hughes, 1969)
L. balthica	19	16.01	11.5-21.68	4.12	Deposit (Olafsson, 1986)

An analysis of variance of $log_{10}(P:G)$ by species revealed significant differences $F_{4,88} = 325$; $\mathbf{p = 0}$, with Tukey's HSD revealing *S. plana* and *F. fabula* to be indistinguishable, and that all other pairs of species are significantly different ($\mathbf{p = 0}$). A box-plot of $log_{10}(P:G)$ for the five Tellinoid species was constructed, including minimum, maximum, median and interquartile ranges (Figure 3.4). The standard deviations of the log of P:G were *D. vittatus*: 0.11; *M. tenuis*: 0.06; *F. fabula*: 0.09; *S. plana*: 0.08; *L. balthica*: 0.04. The range of the P:G ratio recorded for *L. balthica* did not overlap with the range of ratios of any other species. *S. plana* and *F. fabula* are not clearly differentiated in terms of range. *M. tenuis* includes some outliers of higher P:G, and otherwise does not overlap in range with *S. plana*, while *M. tenuis* does overlap with *F. fabula* and *D. vittatus*.

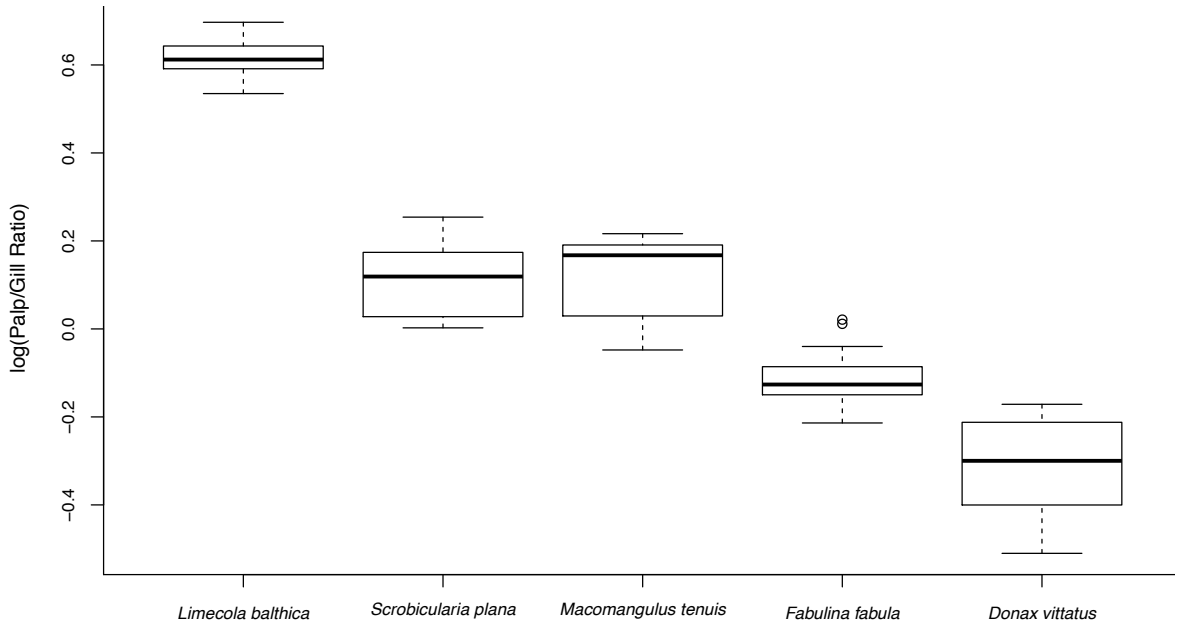


Figure 3.4. Box-plot of P:G for the five species of Tellinoid examined. The box represents the interquartile range, with the median shown by the line in the centre. The whiskers extend to the last data point within 1.5*Interquartile Range of the box. Outliers are indicated using small open circles.

3.3.1 Relationship between gill area, palp area and P:G and dry flesh weight

The relationships between dry flesh weight (mg) (DFW) and gill area, palp area and P:G revealed a significant increase in P:G with DFW in *D. vittatus* (Table 3.2). *D. vittatus*' gill was the only organ for which a significant relationship with DFW was not observed.

Table 3.2. Relationships between palp area, gill area, P:G and Dry Flesh Weight (mg) for the five Tellinoid species examined. Prediction equations from linear relationships $Y = mX + c$ where $Y : X$, are displayed at the top of each column. Regression coefficients (R^2) are displayed underneath regression equations

Species	Gill Area : DFW	Palp Area : DFW	P:G : DFW
Limecola balthica	$y = 22.91x + 2.98$ $R^2 = 0.44$, **p = 0.002** *	$y = 77.08x + 12.81$ $R^2 = 0.41$,**p = 3.4e-3** *	$y = -1.95x + 4.22$ $R^2 = 0.06$
Scrobicularia plana	$y = 132.02x + 16.07$ $R^2 = 0.64$, **p = 7.2e-5** *	$y = 170x + 21.9$ $R^2 = 0.51$, **p = 8.3e-4** *	$y = -0.12x + 1.34$ $R^2 = 0.004$
Fabulina fabula	$y = 279.53x + 2.3$ $R^2 = 0.59$, **p = 4.5e-5** *	$y = 441.54x + 2.37$ $R^2 = 0.64$, **p = 1.4e-5** *	$y = 9.79x + 1.25$ $R^2 = 0.02$
Macomangulus tenuis	$y = 908.04x + 1.31$ $R^2 = 0.59$, **p = 2e-4** *	$y = 657.78x + 1.38$ $R^2 = 0.62$, **p = 6e-5** *	$y = -2.59 + 0.81$ $R^2 = 0.004$
Donax vittatus	$y = 114.69x + 19.35$ $R^2 = 0.17, p = 0.08$	$y = 172.4x + 2.96$ $R^2 = 0.38$, **p = 0.005** *	$y = 4.07x + 0.26$ $R^2 = 0.32$, **p = 0.01** *

Significant differences from the null hypothesis are marked with an asterisk. p-values are quoted for P:G only in case of significant difference from null hypothesis that it does not change with DFW ($y = 0x + c$)

3.3.2 Allometry

In order to test the hypothesis that the growth patterns of gills and palps are isometric, regressions of $log_{10}(Gill\ Area) : log_{10}(Length)$ and $log_{10}(Palp\ Area) : log_{10}(Length)$ were performed. These regressions are equivalent to the characteristic growth equations for the gills and palps. As an example, fitting the regression coefficients α, β in the regression equation $log_{10}G = \alpha + \beta \cdot log_{10}L$ is equivalent to solving $G = 10^{\alpha}L^{\beta}$, or, as α is constant, $G = \kappa \cdot L^{\beta}$. The exponents ($a$,$b$,$c$) and the standard errors of the exponents of the following characteristic growth equations for each species were determined: (Table 3.3).

- Length exponent for Gill Area (a, Equation 3.5)
- Length exponent for Palp Area (b, Equation 3.6)
- Gill Area exponent for Palp Area (c, Equation 3.7)

$$Gill\ Area = i.Length^{a} \tag{3.5}$$

$$Palp\ Area = j.Length^{b} \tag{3.6}$$

$$Palp\ Area = k.Gill\ Area^{c} \tag{3.7}$$

The constants i, j, k, l, m of the characteristic growth equations 3.5 — 3.9 are not of interest for the purposes of allometry, as they represent the differences in palp area or gill area between a standard sized animal of each species, and would differ between species even in the case of isometry.

Table 3.3. Exponents for relationships of gill area against length, palp area against length, and palp area against gill area, with standard errors and a length range for specimens used

There are no significant differences from isometric relationships

			Palp:Gill		
Species	n	Length Range	c	S.E.(c)	R^2
Limecola balthica	19	11.5-21.68	0.91	0.048	0.98
Scrobicularia plana	18	13.54-46.82	0.99	0.046	0.97
Fabulina fabula	21	6.53-13.92	0.81	0.15	0.89
Macomangulus tenuis	17	8.95-15.76	1.02	0.17	0.77
Donax vittatus	19	19.06-24.18	1.42	0.32	0.73

	Gill:Length			Palp:Length		
Species	a	S.E.(a)	R^2	b	S.E.(b)	R^2
Limecola balthica	2.05	0.36	0.81	2.02	0.3	0.85
Scrobicularia plana	2.16	0.08	0.99	2.24	0.14	0.97
Fabulina fabula	1.57	0.26	0.81	1.68	0.26	0.83
Macomangulus tenuis	1.9	0.46	0.63	2.01	0.63	0.65
Donax vittatus	1.66	0.56	0.58	3.71	1.01	0.67

The expected value of a and b (Table 3.3) in the case of isometry is 2, as these are area-to-length relations, however c has an expected value of 1 as it relates an area to an area. All relationships show no significant difference from isometry at the $\alpha = 0.05$ level using this method. *L. balthica* and *M. tenuis* grow near-isometrically, with coefficients of 2.05 and 2.02, and 1.9 and 2.01 respectively for gills and palps. *F. fabula* and *S. plana* each have similar growth rates for both gills and palps: 1.57 and 1.69, and 2.16 and 2.24 respectively. While the growth rates of gills and palps in *D. vittatus* appear to differ from 2, these differences are not significant, owing to the variability in the data (coefficient for palps is 3.71, $\mathbf{p = 0.11}$).

Allometric relationships of gill area and palp area to DFW were also examined: (Table 3.4)

- DFW exponent of gill area (d, Equation 3.8)
- DFW exponent of palp area (e, Equation 3.9)

$$Gill\ Area = l.DFW^d \tag{3.8}$$

$$Palp\ Area = m.DFW^e \tag{3.9}$$

Table 3.4. Exponents for exponential growth relationships of gill area (d) and palp area (e) against DFW, with Standard Errors, for specimens used. Asterisk denotes significant difference from isometric relationship exponent of 0.67

	Gill:DFW			Palp:DFW		
Species	d	S.E.(d)	R^2	e	S.E.(e)	R^2
Limecola balthica	**0.43**	0.11	0.7	**0.41**	0.1	0.72
Scrobicularia plana	0.62	0.06	0.94	0.64	0.07	0.91
Fabulina fabula	0.61	0.09	0.84	0.63	0.1	0.82
Macomangulus tenuis	0.79	0.23	0.74	0.79	0.19	0.82
Donax vittatus	**0.28**	0.14	0.43	0.80	0.24	0.62

The expected value of d and e in table 3.4 in the case of isometry is 0.67, as these are area-to-mass (volume) relationships. *L. balthica* differs from isometry for both gill and palp area, with the $Gill\ Area : DFW$ and $Palp\ Area : DFW$ relationships being similar, while *D. vittatus* has significantly sub-isometric increase in gill area with DFW at the $\alpha = 0.05$

level ($\mathbf{p = 0.012}$). *D. vittatus*' gill area increased significantly more slowly than expected with increases in DFW.

The increase of gill area with increasing body mass (DFW) in both *D. vittatus* and *L. balthica* is less pronounced than other species (Figure 3.5). As there is no consistent cross-species relationship between gill area and dry flesh weight, it is not the case that an individual of a particular body mass has the same gill area regardless of species. As there was similarly no cross species relationship between gill area and length, this was not influenced by body condition or spawning.

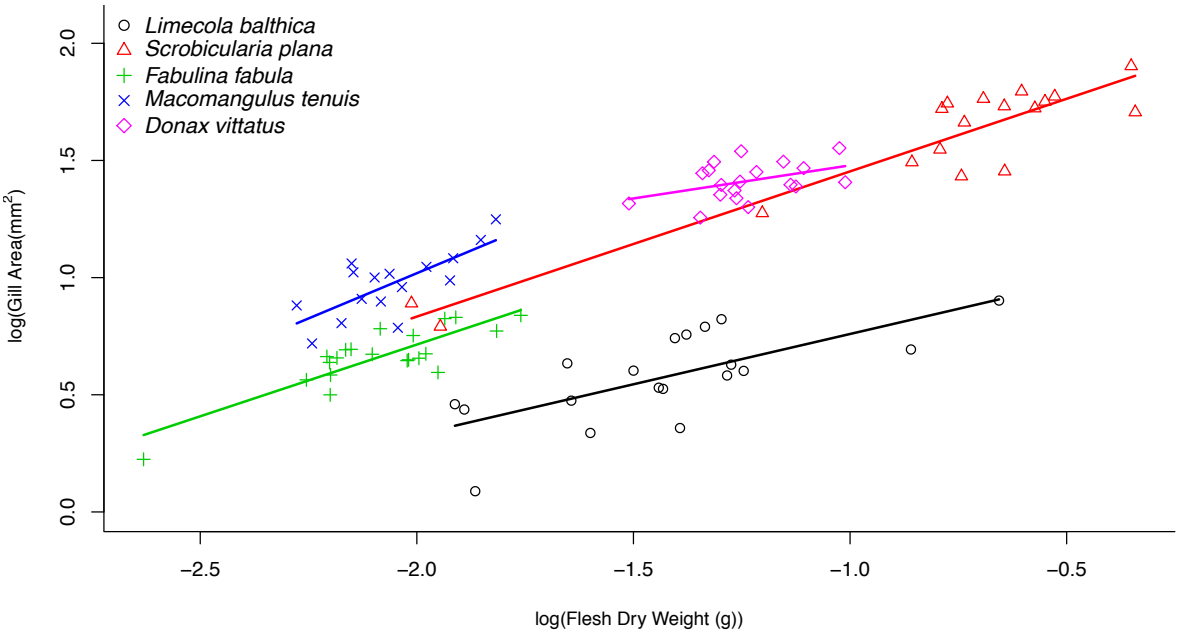


Figure 3.5. Relationship between log_{10}(Gill area $[mm^2]$) and log_{10}(Dry Flesh Weight$[g]$) in five species of Tellinoid bivalves

With the exception of *D. vittatus* , the relationship between Dry Flesh Weight (DFW) and palp area (Figure 3.6) is similar to that for gill area (Figure 3.5), with *L. balthica* having palp growth significantly below that predicted by isometry (*i.e.* heavier individuals have proportionally smaller gills), and all others not significantly different from isometric growth. *D. vittatus* on the other hand, had slightly, but not significantly greater than isometric increases in palp area with DFW.

Comparison of P:G to dry flesh weight reveals no significant change in P:G with body size in any species other than *D. vittatus*, which has a strong increase in P:G with increasing DFW (Figure 3.7). It is clear that the spread seen in P:G in the other Tellinoid species is not owing to any relationship with mass, and within *D. vittatus*, the range of P:G at $x = -1.3$ is

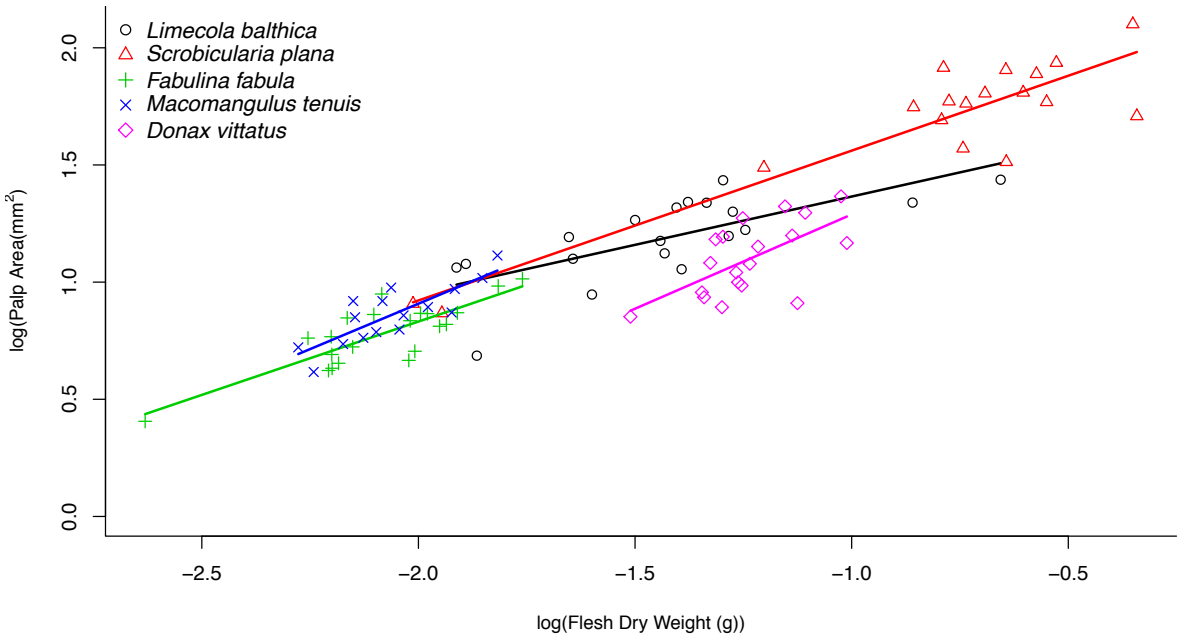


Figure 3.6. Relationship between log_{10}(Palp area $[mm^2]$) and log_{10}(Dry Flesh Weight$[g]$) in five species of Tellinoid bivalves

almost as wide as the overall range.

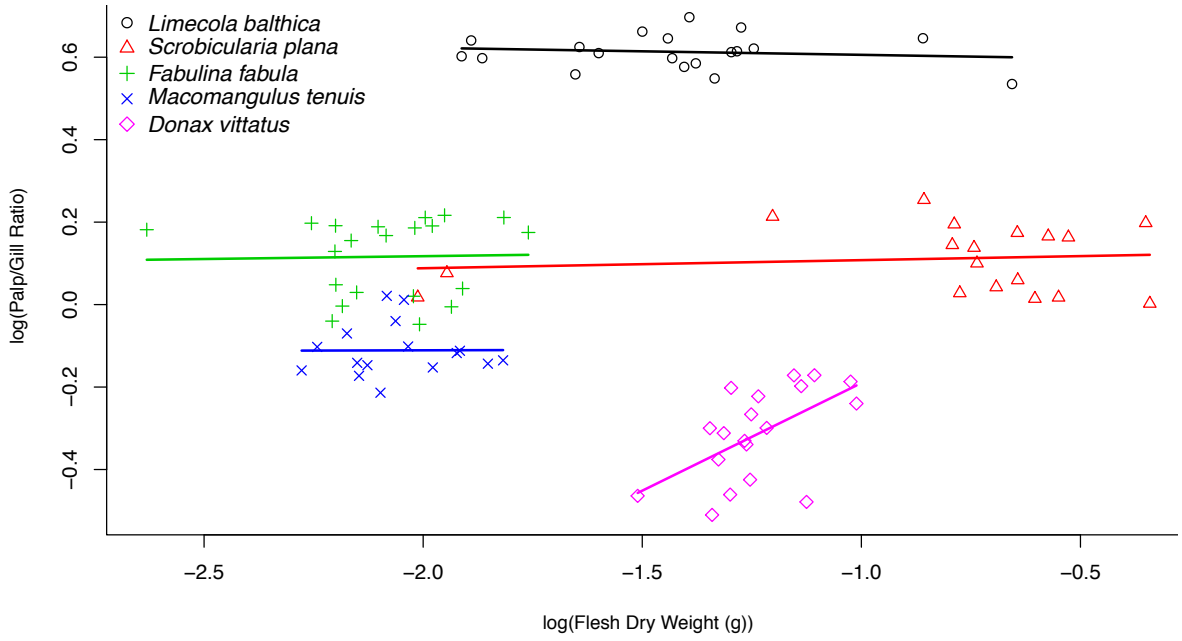


Figure 3.7. Relationship between log_{10}(P:G) and log_{10}(Dry Flesh Weight[g]) in five species of Tellinoid bivalves

As both gill and palp area would be expected to increase with DFW within any particular species, *i.e.* as the animal grows the gills and palps grow, palp area and gill area were plotted

against each other, by species (Figure 3.8). A strong and similar correlation (allowing for differing base P:G for a standard animal of different species) exists in several of the species (and would be expected to as both organs increase with size). The similar slope of the four Tellinoid species is owing to a relationship close to isometry, and is expected, however *D. vittatus*, with a higher slope, does not share this otherwise consistent relationship across the Tellinoids examined here.

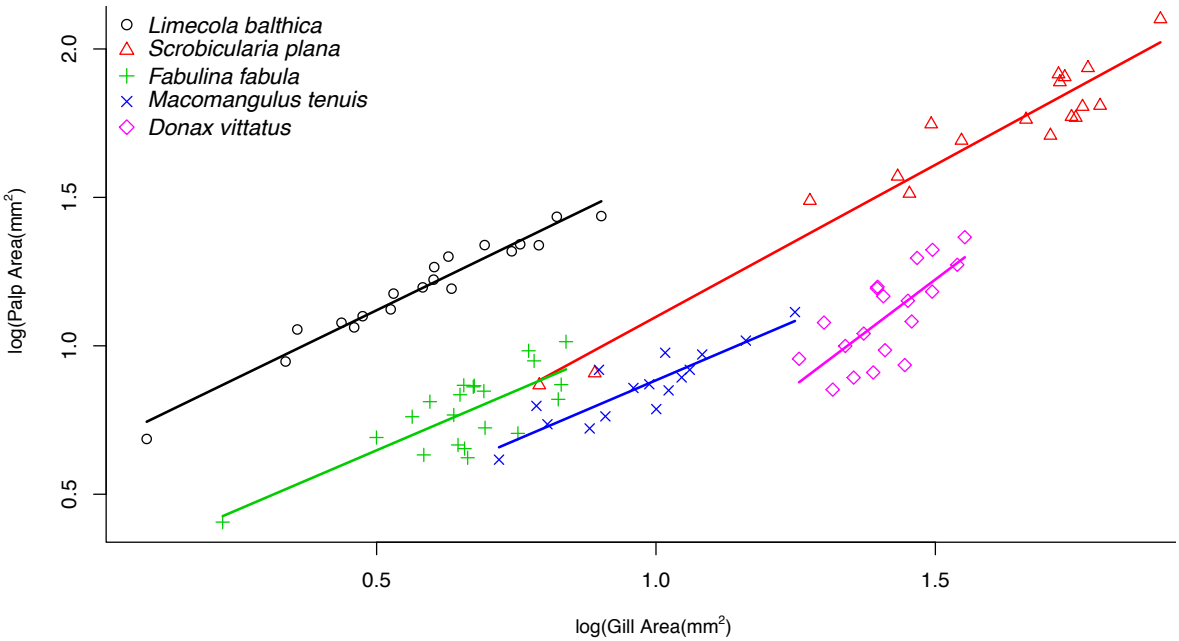


Figure 3.8. Relationship between log_{10}(Palp area $[mm^2]$) and log_{10}(Gill area $[mm^2]$) in five species of Tellinoid bivalves

3.4 Discussion

3.4.1 Palp area to gill area ratio

L. balthica had a high P:G. At the other end of the range, *D. vittatus* had the lowest P:G. P:G results largely agree with given classifications of feeding mode from the literature (Table 3.5), *M. tenuis* more clearly distinguished as primarily suspension feeders, agreeing with previous observations (Wilson, 1990). Results classify *D. vittatus* and *M. tenuis* as principally suspensivores; *F. fabula*, like *S. plana* as both suspension and deposit feeding; and *L. balthica* as principally deposivorous. It is somewhat surprising that *S. plana* and *L. balthica* do not overlap in their range of P:G, considering their significant overlap seen in other work (Compton *et al.*, 2007), as well as the accepted classification of both as deposivores.

Table 3.5. Accepted classification of Tellinoids from the literature and from this work and P:G, where larger palps than gills were taken to indicate some deposit feeding, i.e. $P : G > 1$. References listed in table 3.1.

Species	P:G	Feeding Mode	
Species		Literature	This work
Donax vittatus	0.5	Suspension	Suspension
Macomangulus tenuis	0.78	Suspension/Deposit	Suspension
Fabulina fabula	1.31	Suspension/Deposit	Suspension/Deposit
Scrobicularia plana	1.38	Deposit	Suspension/Deposit
Limecola balthica	4.12	Deposit	Deposit

The results from this study largely agree - in order but not exactly in magnitude - with Compton *et al.*'s (2007) work (Tables A.1, A.2 in appendix A). The main difference in findings between this work and Compton *et al.*'s (2007) is the degree to which *L. balthica* and *S. plana* occupy separate morphospaces (a dimension of their niches). In this work the ratios are clearly distinct, while in Compton's they overlap to a large degree with one another.

The difference in results for *S. plana* and *L. balthica* from those reported by Compton *et al.* (2007) could be explained by variability in environmental conditions (with respect to the Dutch Wadden Sea) leading to different feeding modes (Bayne, 1998). As *S. plana* and *L. balthica* are overlapping in current distribution in Dublin Bay, it is possible that they have specialised their niches somewhat to limit potential interspecific competition (Fenchel, 1975). This does not need to have occurred over an evolutionary time-scale, as Tellinoids

including *L. balthica* display phenotypic plasticity with reference to feeding mode, sediment type, and P:G ratio (Drent *et al.*, 2004). Substantial differences in physiology and behaviour between geographically separate populations of the same bivalve species (*Mytilus edulis*) have also previously been recorded (Kiørboe and Møhlenberg, 1981). *M. tenuis* and *F. fabula* are phylogenetically close, and are conventionally classified according to the same feeding behaviour, as facultative suspension/deposit feeders. As with *L. balthica* and *S. plana*, the ranges of *M. tenuis* and *F. fabula* largely overlap in Dublin Bay, and the difference between the species may be owing to a separation of niches where their ranges overlap. As *F. fabula* is less successful in the littoral environment in Dublin Bay, it is possible that it has adjusted its feeding behaviour to reduce competition with the more successful (in the littoral) *M. tenuis*.

3.4.1.1 Relationship between gill area, palp area and P:G dry flesh weight

In terms of palp area versus gill area, *F. fabula* and *S. plana* have similar P:G ratios, and a similar trend in the relationship, as represented by the slope of the fitted regression line (Figure 3.8). *F. fabula* and *S. plana* are not differentiated by this niche dimension, so as they are not found sympatrically, their niches must differ in one or more other dimensions. *D. vittatus*, due principally to its increase in palp area with length, has a different slope from the other species, which all have a similar slope (Figure 3.8), suggesting its ratio and possibly feeding mode may change as it grows.

3.4.1.2 Allometry

In contrast to the significant increase of P:G with DFW observed in *D. vittatus*, results of allometric equations for *D. vittatus* were inconclusive. The allometric exponent for palp and gill area in *D. vittatus* was not significantly different from 1.0, *i.e.* the assumption of isometry of the relationship between palp and gill areas was not rejected, despite the significant correlation between P:G and DFW. The high intraspecific variability and limited range of lengths encountered does not allow conclusive determination of the existence or otherwise of a relationship, so further work, examining a wide range of animal lengths, is needed. The increase in P:G of *D. vittatus* with DFW is unlikely to indicate a change in feeding mode with increased length, as this would not be possible owing to its short siphons. The correlations of gill area and palp area with total shell length for *D. vittatus* were poorest however ($R^2 = 0.17$, $R^2 = 0.38$ respectively), with no significant relationship between area and DFW ($\mathbf{p = 0.08}$). This could be owing to high intraspecific variability,

potentially indicative of broad niche width for the species, or an artefact of the limited range of specimen lengths. If not such an artefact, however, it represents either a requirement to capture more food, relative to metabolic rate, or a greater degree of selectivity in large *D. vittatus*. The requirement to capture more food or a greater degree of selectivity are apparent possibilities which could require an increase in palp function. An increased degree of selectivity would contradict Levinton's (1971) prediction that, as an obligate suspensivore, *D. vittatus* is effectively nonselective in particle capture.

Gills and palps are food acquisition organs, therefore their effective size determines food intake of the animal, a potentially limiting factor for growth and metabolism. The effective size of these organs is area based, proportional to $DFW^{0.67}$, for example pumping rate is proportional to gill area (Hughes, 1969). For this reason they are expected to scale with metabolic rate. Metabolic rate increases with an isometric mass exponent of 0.67 (Calow, 1981). As metabolic rate is expected to scale with $DFW^{0.67}$, isometric growth of gills and palps should provide a consistent food intake proportional to energetic requirements. Metabolic requirements scaling with size should therefore not be a driver of allometric growth, supporting the theory that differential organ growth rates of gills and palps would represent a change in feeding strategy with size. There was no relationship between total shell length and P:G in the five species examined, so differences in P:G among species are not owing to a cross species allometric growth pattern.

The sub-isometric growth of palps and gills relative to DFW (*i.e.* mass exponents < 0.67) recorded for *L. balthica* was not noted in relation to total shell length. The largest two animals were outliers of significantly greater DFW in proportion to their length however, and thus exerted a disproportionate influence on the regression least-squares equation. When omitted from the data, no significant deviation from isometry was found, however, in order to extend predictions regarding *L. balthica* to animals of this size, further research, including a greater number of large specimens, would be needed to determine whether the species' gills and palps do indeed grow sub-isometrically with DFW.

The hypothesis that P:G ratio does not change with size (Salzwedel, 1979) was rejected for *D. vittatus*, albeit a result not confirmed by the characteristic growth equations. The increased variability of direct palp to gill comparisons, however, resulted in an apparent but insignificant allometric growth result. Further study is needed to determine the nature of *D. vittatus* gill and palp growth. P:G ratio of *D. vittatus* increases with size. This, however, may be driven by metabolic requirements, as *D. vittatus* is an energetic species, with higher

respiration for the same DFW than *M. tenuis* (Ansell, 1973; Trevallion, 1971). *D. vittatus* may require a big gill when younger to provide oxygen for such movement, but conserve energy and food resources for reproduction when older. This would explain it requiring relatively smaller gills when older, as evidenced by the significantly less than expected increase in gill area with DFW as well as relatively larger palps to more efficiently sort food from captured material. No significant deviations from isometry were discerned in *S. plana*, *M. tenuis* or*F. fabula*.

Allometric growth with respect to length Based on the understanding that gills and palps efficacy are defined by their surface area, scaling with power $\frac{2}{3}$ of volume of gills or palps and the fact that intraspecific metabolic requirement scales with power $\frac{2}{3}$ of mass (with mass and volume being closely related) it was expected that gill area and palp area would scale isometrically *i.e.* their area is proportional to the square of length. This was found to be the case in all species examined. The results are consistent with the hypothesis that the growth in these bivalves is isometric. None of the results fell outside the 95% confidence interval for isometry.

No significant morphological evidence for a strategy shift was evident for *T.fabula*, as had been observed by Salzwedel (1979); this may have been owing to a lack of smaller specimens.

Relationship to phylogeny The Tellinoids have a late evolutionary stage suspension feeding common ancestor (Section 1.2.2; Figure 1.3). There was no relationship between genetic relatedness and gill area for a given shell length, with close relatives in the Tellinidae accounting for most of the variation in gill area for a given shell length. As *M. tenuis* and *L. balthica* are in the same family (Tellinidae), and *L. balthica* is more different from *M. tenuis* in terms of P:G than *D. vittatus* or *S. plana*, the between-family variation in P:G is not greater than within-family variation. There appears to be no relationship between relatedness and similarity of P:G.

3.4.2 Ecology of Tellinoids

3.4.2.1 P:G ratio and niche determination

Examining the P:G for *L. balthica*, *S. plana* and *M. tenuis* in this thesis and comparing them with that found by Compton *et al.* (2007), the principal difference appears to be *L. balthica*, which has larger palps and smaller gills than the other Tellinoid species examined to a greater extent than noted by Compton *et al.*'s (2007) work. This suggests a greater

degree of deposivory and detritivory, as opposed to pelagic plankton consumption. The high organic input from the sewage treatment for Dublin (Wilson *et al.*, 2007) may explain this difference; with detritivory perhaps offering a a richer niche in Dublin Bay compared to other habitats, depending on the proportion of material that settles out and is therefore available to deposivores, versus the proportion which remains suspended in the water column available for suspensivores.

3.4.2.2 Potential applications of P:G to niche differentiation

From the point of view of P:G, there are two broad niches, suspension and deposit feeding, and an indication of the degree to which each species occupies each niche. P:G can be used for classification of feeding of lamellibranch bivalves. Within deposit feeders there are expected to be several niches (Levinton, 1972), for example the niche division observed in Hydrobia (Fenchel *et al.*, 1975), with the same not being true for suspension feeders. If niches were defined in terms of variation in Log(P:G) then it would be expected that the range of variation in this ratio would be smaller for deposivores than for suspensivores. While *D. vittatus* has the largest standard deviation, at 0.11, and *L. balthica* a small sd of 0.04, the sd of *M. tenuis*, at 0.06 being smaller than those of *F. fabula* and *S. plana*, at 0.09 and 0.08 respectively, run counter to this argument (Figure 3.8).

3.4.3 Internal morphology and its relationship to feeding type

3.4.3.1 Bioenergetics

It was found that *S. plana* had a lower P:G than expected, indicating it being less of a deposit feeder than expected. The type of feeding can affect bioenergetics, as certain types of feeding are more energy intensive than others and the amount of energy spent by the gill drawing through food is affected by the type of feeding behaviour. *D. vittatus* 's high metabolic rate can account for higher energy expenditure than the other species (other metabolic rates). It is possible that *S. plana* in Dublin is more energetic, needing a larger gill for respiration. The primary alternative explanation is that *S. plana* is engaging in more suspension feeding and therefore ingesting a greater organic proportion, which, with its associated reduction in overall ingested volume for the same calorific value, results in smaller requirements for palps. This apparent difference in strategy in Dublin Bay reduces its potential competition with *L. balthica*, and while it brings its P:G in line with *F. fabula*, it does not materially increase its potential competition with *F. fabula*, as the two are not found in the same locations.

3.4.3.2 Feeding adaptations

There was mixed evidence of a change in ratio with size for *D. vittatus*, with the allometric equation coefficient being insignificant despite the significant correlation between P:G and DFW ($\mathbf{p = 0.01}$). If P:G does in fact decline with size in *D. vittatus*, this could indicate a diversion of resources away from energy intensive metabolism towards reproduction and gametogenesis. It is also possible for an animal to both suspension and deposit feed. An increase in P:G was found for *D. vittatus* with size. Young bivalves grow fast converting all their energy into somatic growth; this shifts to reproduction with increase in size (Rodhouse *et al.*, 1986). Given the short length of the siphons of *D. vittatus* (thought to indicate obligate suspensivory) it is not as well adapted to a different form of feeding, if the increase in P:G with DFW is not a chance correlation (α error is expected with $p = 0.05$), then some other factor must explain it, and perhaps deposit feeding is possible.

Shifts in feeding strategy are found in bivalves. In species known to suspension and deposit feed, such as *M. tenuis* and *S. plana*, a shift in P:G would likely indicate a feeding change with age. This would present as a change in P:G with total shell length; no such trend, however, is found in data here.

3.4.3.3 Other possible influences on P:G and feeding mode

Gill size may be indicative of the proportion of time spent covered by water. *M. tenuis* were collected for this study from a location in the upper intertidal, covered by water for approximately 40% of the tidal cycle. *F. fabula* on the other hand were collected from close to the spring low water mark, and from channels in the low intertidal which are covered $> 90\%$ of the time. *S. plana* and *L. balthica* were collected from the mid-tidal flats which are covered for 40-50% of the tidal cycle. *D. vittatus* were collected close to the spring low water mark, and were immersed for in excess of 95% of the tidal cycle. The difference in gill area between *M. tenuis* and *F. fabula* could be partly driven by the need for *M. tenuis* to pump a sufficient quantity of water while immersed. The greater difference between *L. balthica* and *S. plana* than observed elsewhere could also be related to time spent immersed. There is, however, evidence that Tellinoids including *L. balthica* draw in interstitial water through their siphon channels even when not covered by water, although this leaves them vulnerable to siphon cropping by birds as well as by fish and crabs (De Goeij *et al.*, 2001).

3.4.4 Conclusions

The degree of difference between the area of palps of *F. fabula* and *M. tenuis* was not as large as that seen previously (Wilson, 1990). The distinction between the two species in terms of P:G was still clearly evident however. It is possible that differences between *M. tenuis* and *F. fabula* and between *S. plana* and *L. balthica* respectively are being driven by a reduction in niche overlap in terms of feeding mode to reduce potential competition.

The P:G area was established for the littoral Tellinoids of Dublin Bay. *D. vittatus* and *M. tenuis* were classified as suspensivores, *L. balthica* was classified as deposivorous, and *F. fabula* and *S. plana* as using both feeding modes.

Chapter 4

Diet Composition Determination by Crystalline Style Examination in Five Tellinoid Species from Dublin Bay

Abstract

A comparative dietary analysis of five species of Tellinoids in their natural habitats was determined by examination of the plankton shape and size present on the crystalline style. The plankton composition on the crystalline style was taken as a proxy for the diet composition of the bivalve. Dietary overlap was inferred from the breakdown of results by size and shape of plankton in the five bivalve species examined. In order to determine the importance of each type of plankton in the diet of each species, the energy content of the total material found on the crystalline style was quantified. Presence or absence of plankton morphospecies was significantly different among the species examined. In energy terms the species also differed significantly, in shape and size of plankton consumed. In all species except *Scrobicularia plana*, in excess of 65% of the energy content was provided by spherical and rectangular shaped plankton. The crystalline style contents of *Donax vittatus* were dominated by picoplankton (< 2 μm), which also constituted a substantial proportion of the diet of *Macomangulus tenuis*, *Fabulina fabula* and *S. plana*, but were a minor constituent of *Limecola balthica*'s diet. Foraminifera were found on the crystalline style of *L. balthica* , a previously

undocumented occurrence.

4.1 Introduction

The analysis of the diet composition and preferences of bivalves is useful in determining the source of their food and in defining niches, in terms of plankton morphospecies (shape and size). Morphospecies identification involves the discrimination between taxa based on readily observable characteristics (Derraik *et al.*, 2002), and has previously been used to classify algae as well as cyanobacteria (Rejmánková *et al.*, 2004). A diet with low diversity can indicate specialisation (Elliott *et al.*, 2002) whereas a wide variety of food items is generally indicative of opportunistic feeding (Smith *et al.*, 1984). Dietary analysis is considered to be useful in differentiating between deposit feeders and suspension feeders. It is expected that suspensivores who feed indiscriminately from the water column should consume a wider variety of morphospecies than deposivores (Levinton, 1972).

Suspension-feeding and deposit-feeding bivalves are important components of marine ecosystems. In estuaries, bivalves are the most dominant component of the macrobenthos, and play a significant role in ecosystem processes (Dame, 1996; Asmus and Asmus, 2005). Large amounts of particulate matter are cycled in the estuarine system through bivalves (Smaal and Prins, 1993). Particulate matter is ultimately processed and converted into flesh and gametes, deposited in the benthos as faeces and cycled from complex molecules into inorganic forms which support further phytoplankton/food production (Newell and Koch, 2004; Ward and Shumway, 2004). Investigating this bivalve feeding behaviour elucidates the nutrient recycling pathways in marine systems. Bivalve feeding and movement affects sediment structure by bioturbation and sediment re-working (Rhoads, 1963; Zardus, 2002). The type of feeding undertaken by bivalves, deposit or suspension, defines their impact on the system.

The dietary habits in terms of morphospecies of a range of the Tellinoidea in Dublin Bay are unknown. Generally the investigation of an animal's diet is determined by examination of its stomach contents. Stomach content analysis is a technique used to determine the type of food, which is processed by an individual, *i.e.* its diet (Rouillon *et al.*, 2005). Locating and analysing the stomachs of small bivalves is difficult. The stomach is not always distinct from surrounding tissues in small specimens. Owing to this unreliability, in this investigation the crystalline style, which is located in the stomach of bivalves and readily identifiable, was removed and analysed. The crystalline style is an elongated rod, located in an out-pouching called the crystalline sac. This sac is located just beside the stomach, with its anterior end

jutting into the stomach (Nelson, 1917; Yonge, 1923; Bailey and Worboys, 1960). A large amount of plankton can be found attached to the anterior end of the crystalline style in bivalves (Hawkins *et al.*, 1986), and this is true of the five species investigated here.

Feeding mode describes the mechanism of food transport from an organism's surroundings into the organism (Riisgård and Kamermans, 2001). In bivalves there are two main types of feeding; suspension and deposit. The former can be broken down into either active or passive and the latter into surface or subsurface. Some bivalves are able to use more than one feeding mode. Discrimination between the two main types of feeding mode can be difficult, particularly when looking at stomach contents. This is because of the natural, gradual transition from the food lying on the top layer of the sediment to suspended matter in the water just above the sediment surface (Riisgård and Kamermans, 2001), with some deposit feeders relying partially or completely on suspended food and some suspension feeders collecting food particles at the sediment-water interface, depending on environmental conditions (Ward and Shumway, 2004). Suspensivores and deposivores may rely on the same food source at the same time, irrespective of feeding type (Kamermans, 1994). Discrimination between the two main types of feeding mode can be difficult to discern directly from stomach contents. This is because of the natural gradual transition from the food lying on the top layer of the sediment to suspended matter in the water just above the sediment surface (Riisgård and Kamermans, 2001). *S. plana* are often seen to leave tracks of their siphons on the intertidal sediment surface when the tide is out, indicating deposit feeding (Figure 4.1).

Dietary evaluation and diet overlaps are used to determine if species are dependent on common resources (Kellnreitner *et al.*, 2013). The Tellinoidea use similar resources within their ecosystem and commonly co-occur as they are closely related, morphologically similar species (Schmitt and Coyer, 1982; Delbeek and Williams, 1987). Co-existence of species based on the utilisation of the same resources indicates the potential for competitive interactions between species. Resource partitioning among community members that use similar resources is common, and often occurs along the dimension of habitat, food or time (Schoener, 1974; Garrison and Link, 2000; Root, 1967; Schoener, 1974; MacNally, 1983; Ross, 1986). Resource partitioning can often be a direct result of current or past competition for resources (Delbeek and Williams, 1987).

Suspended particulate organic matter (POM) has been identified as the major source of energy for macrobenthic communities (Sokołowski *et al.*, 2012). POM consists of phytoplankton and detrital particles, sediment particulate organic matter, and microphytobenthos

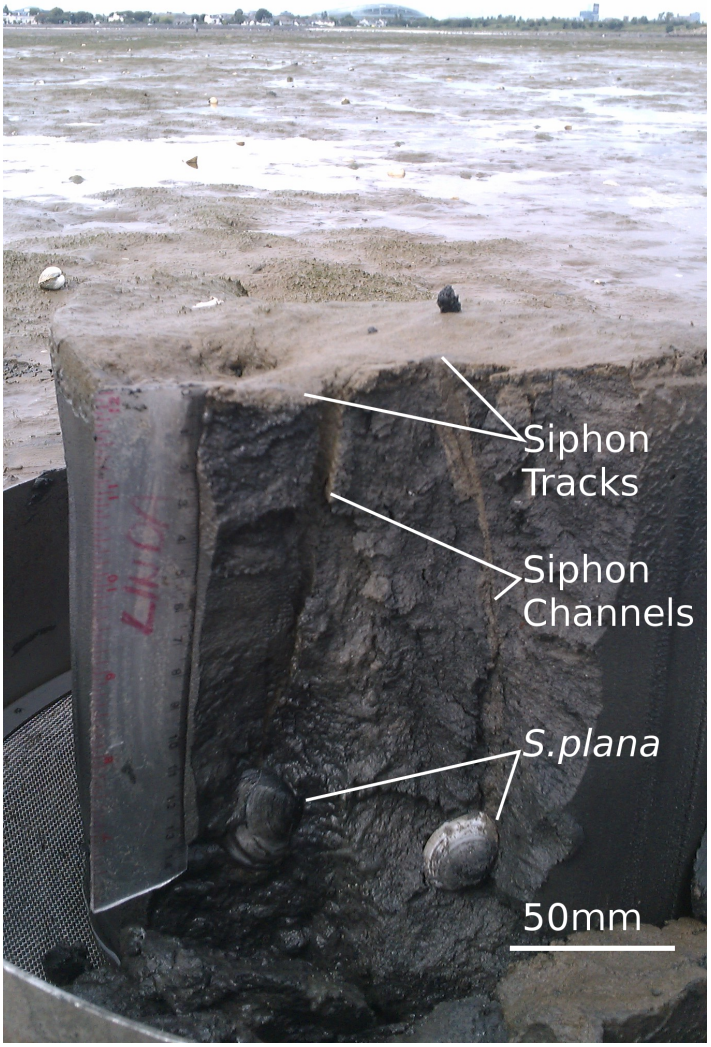


Figure 4.1. *S. plana* buried 12cm deep in intertidal sediment, showing siphon channels and tracks on the sediment surface.

in varying proportions. Identification of all particles to taxonomic species level, as opposed to morphospecies, would be effectively impossible for some detritus particles which may be ingested.

4.1.1 The feeding process

The Tellinoidea (Eulamellibranchia) mainly ingest small phytoplankton and detritus particles (Wilson, 1990). Particles in the range 1–7 μm are preferred (Beecham, 2008), with particles > 4 μm typically retained efficiently (Riisgård, 1988). After plankton is inhaled through the inhalant syphon it gets trapped in mucus on the gill surface and cilia and is moved towards the food groove. The food is then passed down the food groove and to the palps where particles are sorted (this feeding process for gills and palps has been explained in detail (Section 1.2.3)). Acceptable food is passed into the mouth and rejected material is swept to the edge of the mantle. When expelled from the animal these rejected particles constitute pseudofaeces.

4.1.2 The crystalline style

In the stomach, the crystalline style, a transparent rod, rotates against the gastric shield to aid mixing of enzymes with food particles. As the crystalline style is rotated against the gastric shield by the co-ordinated ciliary beat of the stomach and intestinal epithelia, the crystalline style is abraded and dissolved, with digestive enzymes being released. The crystalline style is secreted by the stomach and is largely composed of protein bound to sugars (Gosling, 2008). How the formation of the crystalline style occurs is still unknown (Beninger *et al.*, 1991). The crystalline style sac secretes enzymes that are incorporated into the crystalline style as it is being secreted (Figure 4.2). The resulting food mix including enzymes, passes through the sorting area of the stomach and the finer particles are moved into the digestive glands. Rejected and waste particles from the digestive gland are moved directly into the intestine. The crystalline styles of both deposivores and suspensivores have been found to be the same, with no difference even in terms of digestive enzymes, meaning the crystalline style cannot in itself be used to define feeding type (Gosling, 2008).

In some species of mollusc, the examination of the crystalline style is not possible, owing to the dissolution of the crystalline style following extraction from the body (Nelson, 1917). The examination of the crystalline style in the Tellinoidea is feasible however, as the Tellinoidea have solid crystalline styles when the tide is in or recently ebbed, and these remain solid

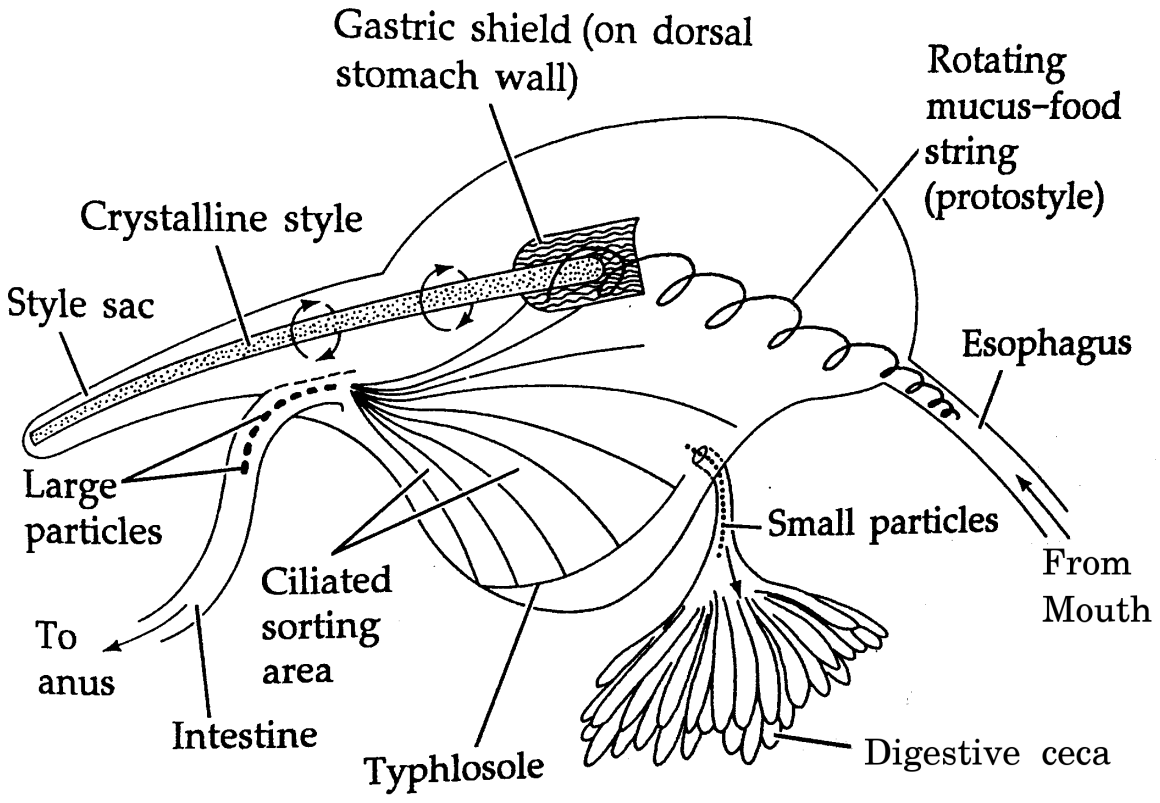


Figure 4.2. A diagram of a bivalve stomach and crystalline style (Brusca and Brusca, 2003)

if the animal is fixed in formalin. As the crystalline style can dissolve within an animal in adverse conditions, and conditions incompatible with feeding, the exact timing of which is unknown for the species studied here, immediate fixation is required (Nelson, 1917). The crystalline styles of all five species of Tellinoids in this investigation were well developed, supporting their classification as herbivorous bivalves (Brock and Kennedy, 1992). Animals for this study were collected during the ebbing tide to ensure that crystalline styles were not partially dissolved, as the styles of some Tellinoids dissolve with the tidal cycle (Hylleberg, 1972).

4.1.3 Aims

The aims of this investigation were to determine plankton morophospecies composition in the diet of five species of Tellinoids, and to establish dietary overlap between the Tellinoidea of Dublin Bay.

1) H_1: Suspension feeders ingest a wider variety of plankton sizes and shapes than deposit feeders (Levinton, 1972)

It is predicted that deposivores such as *L. balthica* specialise to consume a limited range

of available prey, while suspensivores such as *D. vittatus* consume a wider variety of prey (Levinton, 1972).

4.2 Methods

Stomach content analysis or dietary analysis requires a sample of ten to fifteen individuals to give an adequate representation of a diet (Hurtubia, 1973); here a similar approach was adopted for crystalline style analysis. In this investigation ten bivalves (of approximately equal size for each species ±10%) of each of the five Tellinoid species were collected and analysed.

4.2.1 Collection of bivalves

Specimens were collected from Dublin Bay on the 8th October 2012 during the ebbing tide. Tellinoids were collected from known sites of high abundance in Dublin Bay and Gormanstown Beach, Balbriggan, shortly after the ebbing tide. *F. fabula* and *M. tenuis* were collected from Blackrock, Dublin Bay (53°30'33.0" N, 6°17'59.5" W). *S. plana* and *L. balthica* were collected from Sandymount, Dublin Bay (53°32'76.7" N, 6°19'64.8" W) and *D. vittatus* was collected from Balbriggan, North County Dublin (53°63'60.4" N, 6°20'80.2" W) (Figure 4.3). A spade was used to take a sample of the sediment which was subsequently placed in a 1mm sieve. The sieve was shaken in sea water to separate the sediment from any bivalves present. Bivalves were then removed and transported to the laboratory, in a bucket containing sediment and water from the collection site as soon as possible *i.e.* always within one hour.

4.2.2 Treatment of bivalves and analysis

All specimens were collected within a three hour period and placed in 10% formalin with 1% Lugol's iodine solution, on site. The abductor mussel of each animal was severed using a scalpel before immersion in 10% formalin, to ensure full fixation of the animal tissue. The preserved specimens were analysed within a two month period from the date of collection. The total shell length (mm), shell depth (mm), shell width (mm) were recorded with a Vernier callipers to 0.01mm for each individual. The wet weight of each individual was recorded to ±0.01 mg using a calibrated Mettler Toledo B154-S analytical balance after blotting the animal on tissue paper. Dry weight (mg) was established by drying in an oven at 105 ± 5 °C for 24 hours and weighing. Animals were then placed in a furnace at 450°C for 6 hours in order to determine loss on ignition and organic matter content and thus ash free dry weight

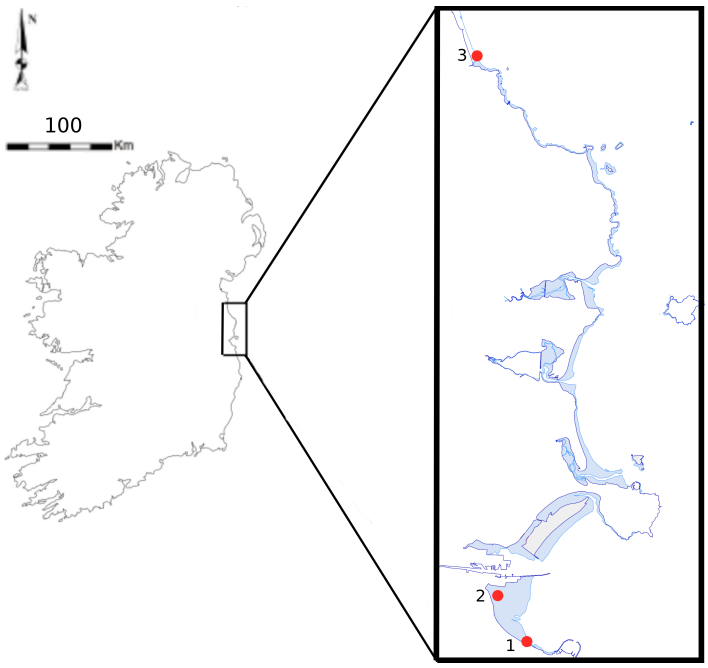


Figure 4.3. Map of Ireland showing the location of the sampling area, with expansion showing sampling locations labelled with red dots: 1: Blackrock, 2: Sandymount, 3: Balbriggan. Map credit Google maps (2017)

(mg) (Velasco *et al.*, 2006). Each animal was dissected and the crystalline style carefully removed. The crystalline style was then placed on a microscope slide and covered in glycerol to prevent desiccation and a cover slip was placed on top for examination under a light microscope (Nikon Eclipse E400). The plankton present on the crystalline style were sketched, measured and their abundance estimated on a specifically developed scale of 1-4 (Figure 4.4) based on the SACFOR scale (Connor *et al.*, 1997). Total manual counts would not have been practical, therefore the abundance measure *frequency_scale* was designed to approximate a logarithmic scale (Equation 4.1). Owing to the impracticality of counting all plankton cells on the style of each animal, and in particular recording the size and shape of each cell encountered, morphospecies described as size-shape pairs were recorded along with an approximate estimate of their frequency of occurrence on each style. A size-shape pair refers to a distinct combination of size and shape of the plankton encountered, so estimates of plankton of size-shape (spheroidal,≈1.5 μm) are recorded separately to either (spheroidal,≈2 μm) or (cylindrical,≈1.5 μm). The descriptive criteria for the frequency estimates are shown in table 4.4, and it was estimated that the classes represent a geometric series with factor 5. This means that a 2 recorded approximately 5 times as many cells of that type as a 1, while a 3

Frequency of sighting	Occasional	Frequent	Common	Abundant
Description as seen through x40 objective lens, light microscope.	Seen once or twice on examination of entire bivalve crystalline style	Seen more than twice, but is not present in half of all field of views, in examination of entire bivalve crystalline style	Seen in more than half of field of views in examination of entire bivalve crystalline style	Is always in field of view, seen in multiples, in examination of entire bivalve crystalline style
Number assigned	1	2	3	4

Figure 4.4. The abundance scale used to determine the frequency of each morphospecies of plankton on an individual crystalline style, adapted from Connor *et al.* (1997). The top row indicates the frequency, the middle row is the determination description used and the bottom row is the *frequency_scale* assigned to each frequency type. This number was then used to approximate the amount of plankton present, using Equation 4.1.

represents 25 times as many as a 1.

$$abundance \approx 5^{frequency\_scale-1} \tag{4.1}$$

In order to produce a meaningful value for total occurrences of a particular morphospecies in each bivalve species, the frequency scores 1, 2, 3, 4 for that morphospecies were replaced with values 1, 5, 25, 125 for each individual animal on whose style they were found. These values were then summed for all animals of that species, and converted into energy as described in equations 4.2–4.4. For each bivalve species, the proportion of each plankton morphospecies in the natural diet was determined by dividing this energy value for the morphospecies by the total energy.

Plankton morphospecies descriptions were carried out using shape descriptions (Figure 4.5). Ten crystalline styles from individuals of each of the following species were analysed; *D. vittatus*, *M. tenuis*, *F. fabula*, *S. plana* and *L. balthica*. A second reader verified a sub-sample of the individual crystalline styles for measurement, description and an approximation of abundance (Olympus BX41 microscope). Volume calculations from plankton shapes were carried out by converting each shape to an appropriate geometric shape, and computing the volume for that shape using the standard formula. The resulting values were converted to

grams of carbon using the ratio (Equation 4.2 from Dalsgaard *et al.* (1997)).

$$1g\ C : 10g\ plankton\ Weight \tag{4.2}$$

Plankton weight is the true wet weight of plankton cells, without extraneous water, which can be computed using the volume of the cells (Equation 4.3), rather than the measured wet weight of a drained sample (Strikland, 1960). Density is estimated to be equal to that of seawater. Energy is determined from grams of Carbon using the formula from Platt and Irwin (1973) (Equation 4.4).

$$plankton\ Weight = cell\ volume * density \tag{4.3}$$

$$Energy\ of\ organic\ Carbon = 47.7Jg^{-1} \tag{4.4}$$

Energy content for each morphospecies in each bivalve species was estimated from the number of distinct observations of each plankton morphospecies in each individual, the frequency of the morphospecies when observed and the size and shape of the morphospecies.

4.2.3 Statistical analysis

Data analysis was carried out in R (R Core Team, 2016). Data were collated for each combination of plankton shape and size range, and also collated separately for all plankton in each size range, and all plankton of each shape. A Fisher's exact test of independence was used to initially analyse whether there were significant differences among species in terms of distinct observations of plankton of each shape. Each distinct observation was the presence of one or more plankton cells of that type (Figure 4.5) in a single animal. A Fisher's exact test of independence of distinct observations of plankton of each size category (Table 4.1) was also carried out.

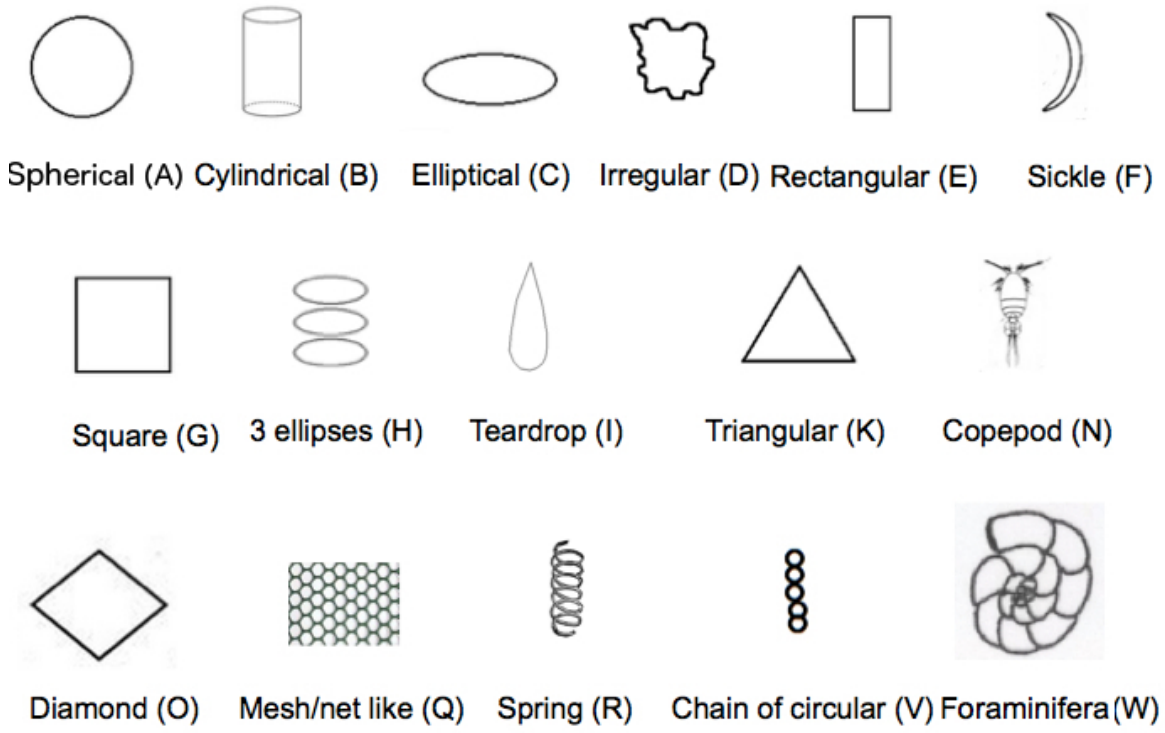


Figure 4.5. Shapes used to describe plankton morphospecies (Derraik *et al.*, 2002) viewed on the crystalline style of Tellinoids from Dublin Bay. Each shape shown here has a description and a corresponding alphabetical descriptor. Shape descriptor letters not shown comprised of shapes that were joined together: three rectangles=J, two cylinders=M, four cylinders=P, four rectangles=S, two ellipse=T, two circles=U, two rectangles=X.

Table 4.1. Distinctions of size class of plankton used in analysis (Adapted from Wehr (1989)).

Plankton size distinctions	
Label	Size
Picoplankton	<2 μm
Small Nanoplankton	2–5 μm
Nanoplankton	5–10 μm
Large Nanoplankton	10–20 μm
Microplankton	20–50 μm

The proportion, by energy content, of plankton of each shape, from crystalline styles of each species were compared using a two-factor ANOVA with interactions. The proportion, by energy content, of plankton of each size category were also compared across bivalve species using an ANOVA.

If there is a relationship or dependency of diet on species, the consumption values for each animal are multiple dependent variables, with the species as a predictor. Permutational multivariate analyses of variance (PERMANOVA) were performed separately for consumption grouped by plankton size as well as by plankton shape. The assumption of homogeneity of multivariate dispersions was validated using a permutational dispersion (PERMDISP) test.

4.3 Results

Plankton morphospecies <5 μm accounted for the bulk of the distinct observations on Tellinoid crystalline styles (Table 4.2). A distinction is apparent between *F. fabula* and *D. vittatus*, with very few morphospecies above 5 μm, and *S. plana* and particularly *L. balthica*, in which a greater number of morphospecies >5 μm were observed. One individual of *L. balthica* had

Table 4.2. plankton data for distinct observations of plankton in all species investigated. Each observation is either a different morphospecies of plankton or from a different individual with respect to every other observation.

Plankton size	Label	*M. tenuis*	*F. fabula*	*D. vittatus*	*S. plana*	*L. balthica*
<2 μm	pico	50	50	32	50	28
2–5 μm	small nano	32	20	16	23	35
5–10 μm	nano	8	0	4	11	19
10–20 μm	large nano	2	3	1	3	7
20–50 μm	micro	0	0	0	0	1

plankton of size >20 μm on its crystalline style. No individuals of other Tellinoid species contained plankton >20 μm on their styles. Foraminifera were also observed on the crystalline style of one individual of *L. balthica*, these were approximately 275 μm but not on the styles of other species (Figure 4.6), they were excluded from further dietary analysis relating to volume.

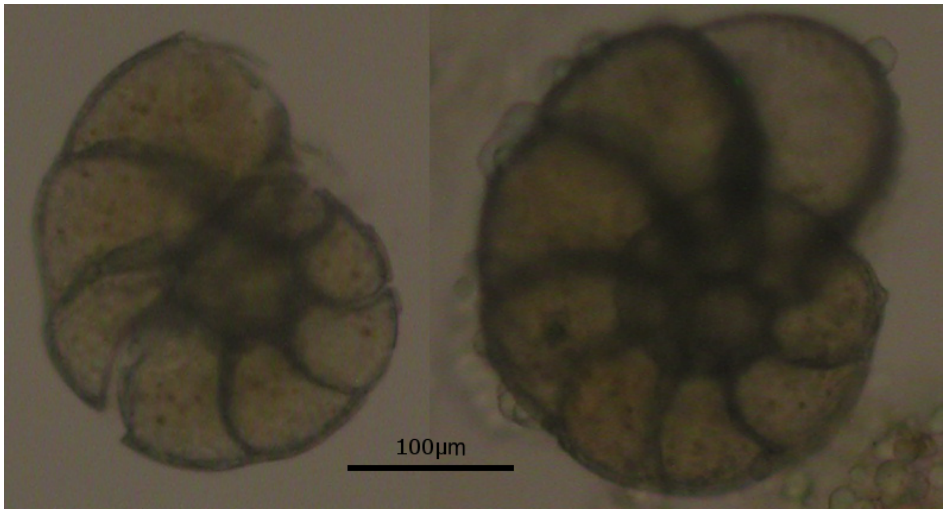
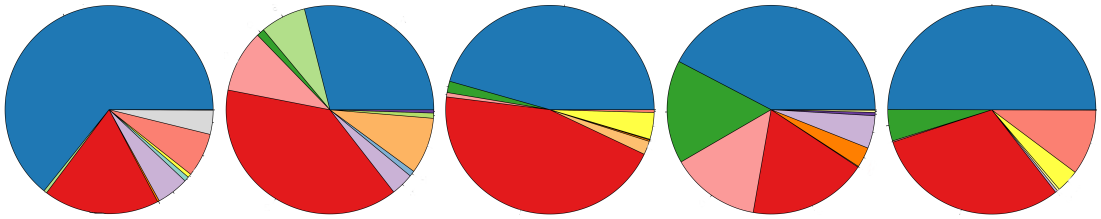


Figure 4.6. Two foraminifera found on the style of *L. balthica*.

A table of the proportion of plankton morphospecies in the diet of each Tellinoid species (Table 4.3) provides an overview of differences in proportions found on the crystalline style. Table 4.3 is limited to the six morphospecies which accounted for the greatest proportion of plankton in the five Tellinoid species examined. Individual charts for each species of bivalve include the nine morphospecies of plankton constituting the greatest proportion, by energy value, of plankton found on that species' crystalline style. A table of proportions of plankton size categories by Tellinoid species (Table 4.4) provides an overview of differences in proportions found on the crystalline style, with detail in individual charts.

Table 4.3. Proportions of each plankton shape, by energy content, found on crystalline style by bivalve species. Shapes accounting for less than 2% of plankton are included in "other" for clarity. A description of the shapes can be found in Figure 4.5.

Shape:	*D. vittatus*	*M. tenuis*	*F. fabula*	*S. plana*	*L. balthica*
A	0.64	0.29	0.46	0.42	0.5
E	0.18	0.39	0.45	0.19	0.3
C	0	0.01	0.02	0.16	0.05
D	0	0.1	0.01	0.14	0
K	0.05	0.04	0	0.05	0
Q	0.07	0	0.01	0	0.1
Other	0.06	0.17	0.05	0.04	0.05

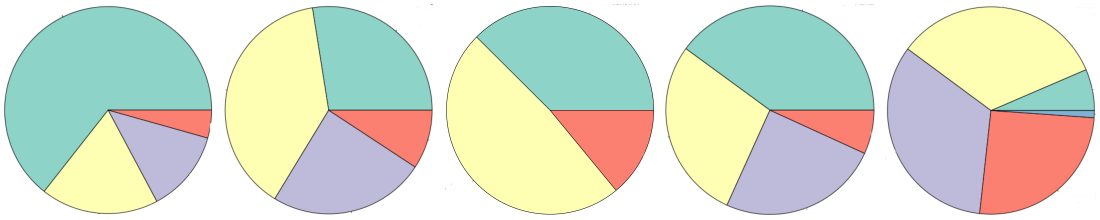


(a) *D. vittatus* (b) *M. tenuis* (c) *F. fabula* (d) *S. plana* (e) *L. balthica*

Figure 4.7. Proportion of the total volume of plankton, by shape, found on the crystalline style of *D. vittatus*, *M. tenuis*, *F. fabula*, *S. plana*and *L. balthica*, respectively. A description of the morphospecies can be found in Figure 4.5, while the full–size graphs with legends are included in Appendix B.1 (Figures B.1,B.3,B.5,B.7 and B.9).

Table 4.4. Table of proportions, by volume, found on crystalline style by species and plankton size category. A description of the size classes can be found in Table 4.1.

plankton size:		*D. vittatus*	*M. tenuis*	*F. fabula*	*S. plana*	*L. balthica*
pico	(< 2 μm)	0.64	0.27	0.38	0.40	0.06
small nano	(2–5 μm)	0.19	0.40	0.48	0.28	0.33
nano	(5–10 μm)	0.13	0.24	0.00	0.25	0.34
large nano	(10–20 μm)	0.04	0.09	0.14	0.07	0.26
micro	(20–50 μm)	0.00	0.00	0.00	0.00	0.01



(a) *D. vittatus* (b) *M. tenuis* (c) *F. fabula* (d) *S. plana* (e) *L. balthica*

Figure 4.8. Proportion of the total volume of plankton, by size found on the crystalline style of *D. vittatus*, *M. tenuis*, *F. fabula*, *S. plana*and *L. balthica*, respectively. A description of the sizes can be found in Figure 4.1, while the full–size graphs with legends are included in Appendix B.1 (Figures B.2,B.4,B.6,B.8 and B.10)

D. vittatus

The plankton found on crystalline styles of *D. vittatus* were dominated by picoplankton to a much greater degree than those found in the other Tellinoids examined, with larger sizes constituting successively smaller proportions of plankton found on the crystalline style (by energy content). *D. vittatus*' style also contained a larger proportion of spherical (A) plankton morphospecies than the styles of the other bivalves (Figures 4.7a, 4.8a).

M. tenuis

The size and shape accounting for the greatest proportion of the contents of the crystalline style of *M. tenuis* were small nanoplankton and rectangular (E) respectively. *M. tenuis*

was the only species on whose crystalline style the spherical morphospecies was not most abundant. *M. tenuis* had approximately equal proportions of picoplankton and nanoplankton, and a small proportion of large nanoplankton (Figures 4.7b, 4.8b).

F. fabula

The contents *F. fabula*'s crystalline style were mostly spherical (A) and rectangular (E) plankton, with other shapes accounting for less than 10% by energy content. In terms of sizes, plankton <5 μm dominate: *F. fabula* derives almost half (48%) of its diet from small nanoplankton, however, in contrast to *M. tenuis*, the remainder of *F. fabula*'s diet consists of smaller particles. *F. fabula*'s diet contains a large proportion of picoplankton (38%), a small proportion of large nanoplankton, and no nanoplankton. *F. fabula* was the only species in which there were no observations of nanoplankton (Figures 4.7c, 4.8c).

S. plana

S. plana had the most evenly spread diet, with four shapes found on its crystalline style each accounting for in excess of 10% of plankton found, by energy content. A broad variety of plankton <20 μm were found on its crystalline style. *S. plana*'s style contents were similar in terms of particle sizes to *M. tenuis*, although slightly shifted towards smaller particles, with picoplankton forming the largest proportion and large nanoplankton being a smaller proportion of its diet (Figures 4.7d, 4.8d).

L. balthica

The crystalline style of *L. balthica* contained 50% spherical plankton. *L. balthica*'s diet was substantially different from the other species, in particular *D. vittatus*, in terms of the proportion of its diet made up of picoplankton ($\mathbf{p < 0.001}$). *L. balthica*'s entire feeding spectrum is shifted towards larger particles. It contained the smallest proportion of picoplankton among the Tellinoids examined, the largest proportion of nanoplankton, large nanoplankton (>10 μm) and the only occurrence of microplankton (>20 μm) (Figures 4.7e, 4.8e).

4.3.1 Comparisons among species

A Fisher's exact test of independence of distinct observations (presence/absence) of plankton of each plankton shape and Tellinoid species was carried out via Monte-Carlo simulation in *R* (R Core Team, 2016) with 10^6 replicates, to determine if the species' diets were significantly

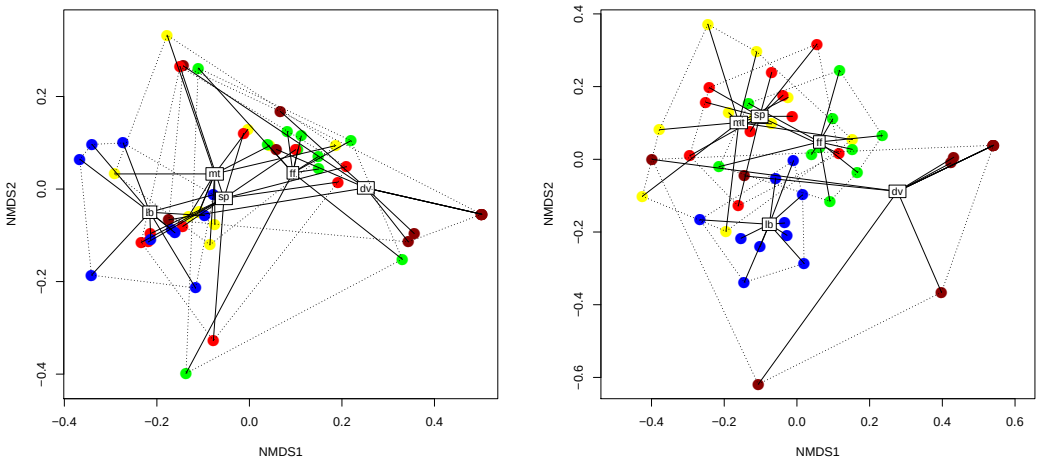
different purely based on the shapes found on each species' styles. The plankton shapes present on the crystalline styles differed significantly with Tellinoid species ($\mathbf{p = 0.0018}$). Separately, a Fisher's exact test of independence of distinct observations of plankton of each size category and Tellinoid species, carried out via Monte-Carlo simulation in R with 10^6 replicates reported no significant difference, with $p = 0.33$, based purely on presence/absence of each plankton size category.

In order to test whether the proportions of each size category found on the style of each Tellinoid varied significantly with the Tellinoid species, an ANOVA was performed of proportions against Tellinoid species and size category. It was necessary to work with proportions, as the raw data were based on a sample from the crystalline style, and not the enumeration of all plankton on the style which would have been impractical. Significant differences were found among the crystalline style contents of the five Tellinoid species in terms of proportions of particles of different sizes (Table 4.5). A similar ANOVA testing whether proportions of shapes found differ by Tellinoid species also recorded significant differences (Table 4.6). The differences in shape were consistent with the results of Fisher's test, with a significant Species:Shape interaction ($F_{88,1035} = 1.42$, $\mathbf{p = 0.008}$). The coefficients of this ANOVA are presented in appendix B.2. The ANOVA of proportions of sizes consumed by species yielded a significant Size:Species interaction ($F_{16,225} = 3.04$, $\mathbf{p = 1e\text{-}4}$, coefficients can be seen in appendix B.3). The proportions in each case were in terms of equivalent grams of carbon (Dalsgaard *et al.*, 1997). The proportions of each shape and size of plankton found on the crystalline style of an individual Tellinoid vary significantly with Tellinoid species.

The significant differences between the natural diets of different species, both in terms of plankton size and shape, were confirmed by the results of permutational multivariate analyses of variance (PERMANOVA) In each case no random permutation among 10,000 generated had a higher F-value (Shape Pseudo-$F_{4,45}$=6.3, $\mathbf{p < 1e\text{-}4}$; Size Pseudo-$F_{4,45}$=5.3, $\mathbf{p < 1e\text{-}4}$).

The differences between species in terms of sizes of plankton in the natural diet, and shapes of plankton are visualised in Non-metric MultiDimensional Scaling plots (Figures 4.9a and 4.9b respectively). Tests of assumptions of homogeneity of dispersion did not reject the assumption for either size or shape data.

The Tellinoid species with the least variety in terms of total number of morphospecies was *F. fabula* with 9; the greatest number of species were found in *D. vittatus* and *S. plana* with 13 each. *M. tenuis* had 12 distinct morphospecies and *L. balthica* 10 distinct morphospecies on their crystalline styles. The average number of morphospecies per individual differed, with



(a) MDS Plot of Plankton Sizes by Species (b) MDS Plot of Plankton Shapes by Species

Table 4.5. ANOVA of Proportions of different sizes of plankton by Tellinoid species. $\Pr(>F)$ is the p value for the observed F-statistic, and stars denote significance at the α level indicated below.

	Df	Sum Sq	Mean Sq	F value	$\Pr(>F)$
Size	4	4.34	1.08	16.36	**9e-12**
Species	4	0.00	0.00	0.00	1
Size:Species	16	3.23	0.20	3.04	**1e-4**
Residuals	225	14.91	0.07		

the fewest, at 2.9, for *D. vittatus*, 4.1 for *F. fabula*, 4.8 each for *M. tenuis* and *L. balthica* and the most, at 5.5 morphospecies, found on the crystalline crystalline style of each individual of *S. plana*.

Table 4.6. ANOVA of Proportions of different shapes of plankton by Tellinoid species. $\Pr(> F)$ is the p value for the observed F-statistic, and stars denote significance at the α level indicated below.

	Df	Sum Sq	Mean Sq	F value	$\Pr(> F)$
Species	4	0.000	0.0000	0.000	1
Shape	22	13.42	0.61	42.05	**<2e-16**
Species:Shape	88	1.82	0.02	1.42	**0.008**
Residuals	1035	15.01	0.014		

4.4 Discussion

Owing to the variability in seasonal and geographic distributions of plankton, and the phenotypic plasticity demonstrated by several bivalves with respect to feeding mode, the data presented are representative only for this particular locality and season, and specifically relate to autumnal plankton. As the plankton encountered were on the outside of a crystalline style, they could not be isolated for separate measurement, so abundance estimations were used together with total observations for each morphospecies for quantification purposes.

4.4.1 Size preferences in the natural environment

The diet of each species was found to vary in composition. *D. vittatus* has a diet dominated by small plankton, with the energy provided by size categories declining with size. *S. plana* also had a diet in which small particles were more important, but to a lesser degree than *D. vittatus*. *F. fabula* and *M. tenuis* both have diets centred on small nanoplankton, however, in contrast to *M. tenuis*, the remainder of *F. fabula*'s diet is skewed towards smaller particles. *L. balthica*'s diet was substantially different from the other species, shifted towards larger particles. Bivalves typically prefer particles of 1–7 μm (Beecham, 2008), and efficiently retain particles >4 μm (Riisgård, 1988), however with the exception of *L. balthica*, a greater proportion of energy intake came from particles <5 μm than those >5 μm. This may indicate that despite preferring and more efficiently capturing larger particles, the picoplankton and small nanoplankton are more important in the natural diet of Dublin Bay Tellinoids. *L. balthica*'s size preference range has previously been described as between 1.5 μm and 15 μm (Self and Jumars, 1978), in line with what is seen here, and in contrast to the greater quantities of smaller particles found in the other species. *S. plana* captures particles >4 μm with close to 100% efficiency (Hughes, 1969). Particle size preferences of the other Tellinoid species has not been previously explored.

4.4.2 Shapes of plankton preferred by Tellinoids from Dublin Bay

The Fisher's test of shapes by species indicates that there are significant differences in the shape of plankton preferred in the diets of the Tellinoids examined, even without considering the quantities in which the various plankton are consumed. Spherical (A) shape dominate the diet, by energy content, of *D. vittatus*, but constitute less than half the proportion in *M. tenuis*, where rectangular shapes form a greater proportion of the diet. *F. fabula* also consumes a large proportion of rectangular plankton. Although *S. plana* and *D. vittatus*

consume far less of the rectangular species than the other Tellinoid species, both spherical and rectangular plankton are consumed in greater quantities than any other plankton type. *S. plana* had the most varied diet, with four shapes having a proportion greater than one tenth of all plankton by energy; *F. fabula* had the least varied diet, with two shapes of plankton morphospecies accounting for almost all its consumption.

Relating the morphospecies variety with feeding behaviours, a diet with low diversity can indicate specialisation (Elliott *et al.*, 2002) whereas a wide variety of food items is generally indicative of opportunistic feeding (Kelley, 1987), which is expected to be characteristic of suspensivores (Levinton, 1972). No consistent relationship following this expected pattern is apparent from the results here, apart from in *M. tenuis*, which is considered to be more of a suspensivore than *F. fabula*, and had a broader diet than *F. fabula*. *S. plana*, which is considered more of a deposivore, had the broadest range of dietary components including those forming $> 10\%$ of its consumption, and *L. balthica*, also considered a deposivore, exhibited no particular specialisation with respect to the other species.

In terms of sizes of plankton particles captured, it was expected that suspension feeders would have a wider variety of particle sizes than deposit feeders (Levinton, 1972), however no significant relationship was found between feeding type and dietary size range. *L. balthica*, a deposivore, had the greatest size range, with *D. vittatus* and *F. fabula* more limited in the particle size ranges found on their styles, and *M. tenuis* and *S. plana* in between. This does not agree with predictions that deposivores such as *L. balthica* specialise to consume a limited range of available particles, while suspensivores such as *D. vittatus* consume a wider variety (Levinton, 1972).

4.4.3 Foraminifera

A previously undocumented observation of two foraminifera in the stomach of *L. balthica* was recorded. *L. balthica* are known to ingest particles as large as 300 μm (Gilbert, 1977). No other species were recorded here as having foraminifera on their crystalline styles. Meiofauna including foraminifera have, however, been previously found in *Macoma nasuta* (Hylleberg and Gallucci, 1975). Investigations into the effect of *L. balthica* on meiofauna noted limited impacts, apart from with copepods, with which they compete for food, however difficulties sorting foraminifera resulted in their exclusion from analysis (Olafsson *et al.*, 1993). Foraminifera are mostly benthic, however some are planktonic, and benthic specimens may also become re-suspended along with sediment, and Tellinoids including *L. balthica* and *S.*

plana are known to ingest sand particles (Hughes, 1970a; Gilbert, 1977). It is of note that sand is sorted and removed from the feeding process as pseudofaeces but these foraminifera specimens were retained.

4.4.4 Potential for larviphagy

The ingestion of larvae from the water is a known occurrence in *Mytilus edulis* (Lehane and Davenport, 2002); this has not been investigated to date in the Tellinoidea. There is little potential for larviphagy to occur in the Tellinoidea, apart from potentially in *L. balthica*, as the size of the Tellinoidean larvae is over 200 μm larger (Jansson *et al.*, 2015) than the size of largest ingested plankton found in this investigation.

4.5 Conclusion

The method of using the crystalline style as a proxy for dietary analysis was successful. A previously undocumented observation of two foraminifera in the stomach of *L. balthica* was recorded. The diet of each species was found to vary in composition. *D. vittatus* has a diet dominated by small plankton. There were significant differences in the shape of plankton preferred in the diets of the Tellinoids examined. No significant relationship was found between feeding type and dietary size range.

Chapter 5

Suspended Particle Capture Efficiency in Terms of Particle Size in Five Species of Tellinoids from Dublin Bay

Abstract

Particle size capture efficiency was used to determine what, if any, size of particles are preferentially captured from suspension by five different species of Tellinoid bivalves in Dublin Bay. The results indicate that large sized particles in suspension are captured more efficiently than small particles by all species. The nature of the relationship is not uniform across species. An inflection point is observed in graphs of Ivlev's electivity index ($\mathbb{E}$) against particle size, and deposit-feeders (*L. balthica*, *F. fabula*, *S. plana*) begin selecting particles, or capturing more efficiently, from a lower size than suspension feeders (*M. tenuis*, *D. vittatus*). *F. fabula* captured a greater proportion of particles from larger size categories than particles in smaller size categories from the available stock suspension. *M. tenuis* exhibited a much weaker linear relationship between size and capture efficiency than *F. fabula*. *D. vittatus*, *S. plana* and *L. balthica* all captured larger particles more efficiently than smaller particles, but the relationship was not linear, with particles over (approx 4.2 μm) captured with approximately equal efficiency, as opposed to the continued increase in efficiency with size seen in *F. fabula* and *M. tenuis*.

5.1 Introduction

5.1.1 The importance of size of particles ingested by the Tellinoidea

Bivalves are ecosystem engineers, playing a major role in the structuring of benthic food web systems, nutrient cycling, modulating the availability of resources to other species and seston consumption (Bayne and Newell, 1983; Langdon, 1990; Asmus and Asmus, 1991; Dame, 1996; Ward and Shumway, 2004). Particle feeding bivalves comprise a large component of the macrobenthic biomass of estuarine systems (Russell-Hunter, 1983; Dame, 1996). The determination of the size of particles captured by bivalves is an important facet of understanding material flow through marine or estuarine ecosystems (Shumway, 1990).

The classic example of resource partitioning and niche division in marine deposivores is between two species of *Hydrobia*: *Hydrobia ulvae* and *Hydrobia ventrosa* (Fenchel and Kofoed, 1976). When these *Hydrobia* species occur allopatrically they exhibit similar particle size preferences, but when they occur sympatrically, one takes slightly bigger particles and one takes slightly smaller particles than when living allopatrically. The *Hydrobia* are partitioning a resource but at the expense of one or both species having to take a non-optimal size. The apparent preferences observed are associations which may have complex positive and negative causes (Underwood *et al.*, 2004). Sympatric species often have evolved to eat particles of different sizes to each other in order to avoid competition (MacArthur and Levins, 1964). What is hypothesised, is that Tellinoids would exhibit exploitative competition. Deposivores may partition to a greater extent than in suspensivores or partial suspension feeders (Levinton, 1971). Co-occurring species that partition a resource will not be expected to consume similar particle sizes, but rather preferentially consume particles of different sizes. If there is an overlap in the size of algae captured by two species this could indicate the potential for partitioning. As all five bivalve species occur in Dublin Bay, it was anticipated that some size preference difference would be seen, reflecting this competitive avoidance. If there is no variation in capture efficiencies, it could mean that the species are not partitioning the resource and may have the potential to colonise more habitats or niches. If two species capture the same size of particle, this indicates a high potential for competition between the two species. If, however, two species predominantly capture different sized particles, this results in less competition between them. As all the species used in this work live in similar habitats, with all five species currently present in Dublin Bay, (*D. vittatus* at very low abundances), it was expected that they would all have differing capture efficiencies in terms of particle size. Any clear indication of selectivity by *D. vittatus* would contradict the theory that, as an obligate

suspensivore, *D. vittatus* is effectively nonselective in particle capture, if the selectivity is not related to a minimum effectively captured size. The ability to efficiently acquire food is dependent on species' adaptive morphology and behaviour in suspension or deposit feeding modes (Stead *et al.*, 2002).

The term capture efficiency (CE) is used to accurately describe the process being measured (Rosa *et al.*, 2015). The removal of particles from suspension is the mechanism of competition, making this more appropriate than metrics utilising post-capture preferences, such as pseudofaecal composition. While previous work, considering post-capture particle preferences, uses a modified form of Ivlev's index to compare retention efficiencies of bivalves (Beals, 2004), the capture of the particle itself, rather than post-capture selection is the driver of competition among suspensivores, as captured particles are no longer available to other feeders; therefore any potential resource partitioning hypothesised among suspensivores must be examined in terms of particle capture rather than post capture selection.

5.1.2 Feeding behaviour

Determining the size preference is an important aspect of characterising feeding, aside from the type of feeding which takes place. Preference for small particles may indicate a tendency towards deposit feeding and muddy habitat dwelling. Conversely, suspension feeders may show no distinction for particle size, ingesting whatever is available.

The suspension feeding bivalves have received more research attention than deposit feeders as they comprise the main commercially valuable species. Particles captured by suspension feeders may be selected (Bayne and Newell, 1983; Beninger *et al.*, 1991; Jorgensen, 1996; Ward and Shumway, 2004) but exactly how this happens is not fully understood. It remains unclear, for example, how *Mercenaria mercenaria* remain non-toxic while *Mytilus edulis* in the same area acquire dangerously high levels of algal-based toxins during toxic algal blooms (algal accumulations) (Shumway, 1990). It has been noted that obligate suspension feeders (*Mytilus edulis*) may adapt the particle size at which they achieve their maximal retention efficiency, reducing it in times when smaller particles dominate the seston, contrary to the widely held belief that suspensivores are nonselective and that retention efficiency is related to immutable physiological characteristics (Strohmeier *et al.*, 2012).

Selection based on the quality of a particle, which was previously thought to only happen post capture, can also happen prior to retention (Yahel *et al.*, 2009) and may differ for different gill and palp types. While retention efficiency may be defined as the particles

which are retained and eaten by the bivalve, the more accepted definition is the reduction in concentration of that particle category between inhalent and exhalent currents in the bivalve. This differential reduction in concentrations of particle types between inhaled and exhaled water, i.e. selective capture, manifests in the decrease in concentration of that particle type in the experimental vessel. Bivalves can exhibit a change in feeding behaviour with season (Strohmeier *et al.*, 2012), so experiments need to be carried out in tandem.

5.1.3 Ivlev's Index

Ivlev's (1961) Index of Electivity, $\mathbb{E}$, a tool used in optimal foraging theory, relates proportion of particles captured to proportion found in the environment, in order to assign a degree of electivity, or preferential capture, of a known prey species by a predator being studied, from -1 (complete avoidance) to +1 (complete selection of an uncommon prey) (Ivlev, 1961). $\mathbb{E} = 0$ represents random feeding, where the animal is consuming prey in proportions found in the environment (Lechowicz, 1982). $\mathbb{E}$ is ideal in a scenario where dense planktonic prey are available and the initial concentration of each prey is known (Strauss, 1979), as was the case here.

Owing to the differences in concentration of the particles in the different size categories, $\mathbb{E}$ was used to compare relative capture efficiencies across all particle size categories and species of bivalve. Other electivity models are available, but Ivlev's is the most commonly used index.

As observed differences in capture efficiency may be imposed by biological constraints, such as the presence of eu-latero frontal cirri, or be based on 'preference', the term capture efficiency is used as the more general term for the observed differences.

In this experiment, the predator is one of the five species of Tellinoid bivalve (with prey being the algal cells, in various size categories). $\mathbb{E}$ is derived from $\frac{r_i - p_i}{r_i + p_i}$ where r_i is percent composition of algae eaten and p_i is percent composition of algae in the initial sample.

Critiques of Ivlev's (1961) index (Jacobs, 1974) have noted that the index is not independent of prey density, however this is not a feature in this study as prey density was controlled by feeding a common algal stock as a prey item, thus excluding this obstacle to its use.

5.1.3.1 Terminology used in this work

For the purposes of this experiment, a time point represents an ordinal description of sampling time during an experiment commencing at Time 0 (T_0), and including, as well as T_0, twenty,

forty, sixty, eighty and one hundred and twenty minutes after T_0 respectively. The Coulter Counter output grouped particles counted into a large number of categories of different size, these were aggregated into a smaller number of categories, where the boundaries were chosen to make the revised category widths as close to 0.4 μm as possible. These revised categories are the size categories referred to throughout this chapter.

Control data represent particle counts sampled from a sampling unit which, while containing no animal, was otherwise treated in the exact same manner, and into which stock solution was added at T_0. Stock Solution was a suspension of preserved unicellular algae. Pyrex beakers (150ml) of height 90mm, used as sampling chambers, were known as sampling units.

A Coulter Counter (Beckman-Coulter, 2009) was used as it is suitable for algal cell counting, as it has the most accurate and time-efficient technology available for sizing and counting particles and cells. It has been used widely in the past in counting unicellular algal cultures, such as *I. galbana* in the technique Scope for Growth used by the International Council for the Exploration of the Sea (ICES) (Widdows and Staff, 2006). The Coulter Counter set-up and parameters are outlined in section 5.2.5.1.

5.1.4 Aims

The objective of this work was to find whether or not five Tellinoid species, with the same body plan, potentially compete for the same size of algal particles in the range of 1.9 μm–20 μm, while suspension feeding. This consumption reflects niche division in terms of captured particle size (Gosling, 2015).

This includes distinguishing between species, if any, that have affinities for large or small particles. Determining whether, as predicted by Levinton (1971), an obligate suspensivore such as *D. vittatus* exhibits no preference within the range of particles it can efficiently capture. Finally, determining which, if any, differences exist between the five species in terms of capture efficiencies for each particle size category.

Formally, the null hypothesis was that preferences for particle sizes do not vary with species (Equation 5.1).

$$H_0 : \mathbb{E}_{a,i} = \mathbb{E}_{b,i} \tag{5.1}$$

$$\forall\ a, b \in \{D.\ vittatus, M.\ tenuis, F.\ fabula, S.\ plana, L.\ balthica\}, \forall i \in particle\ sizes$$

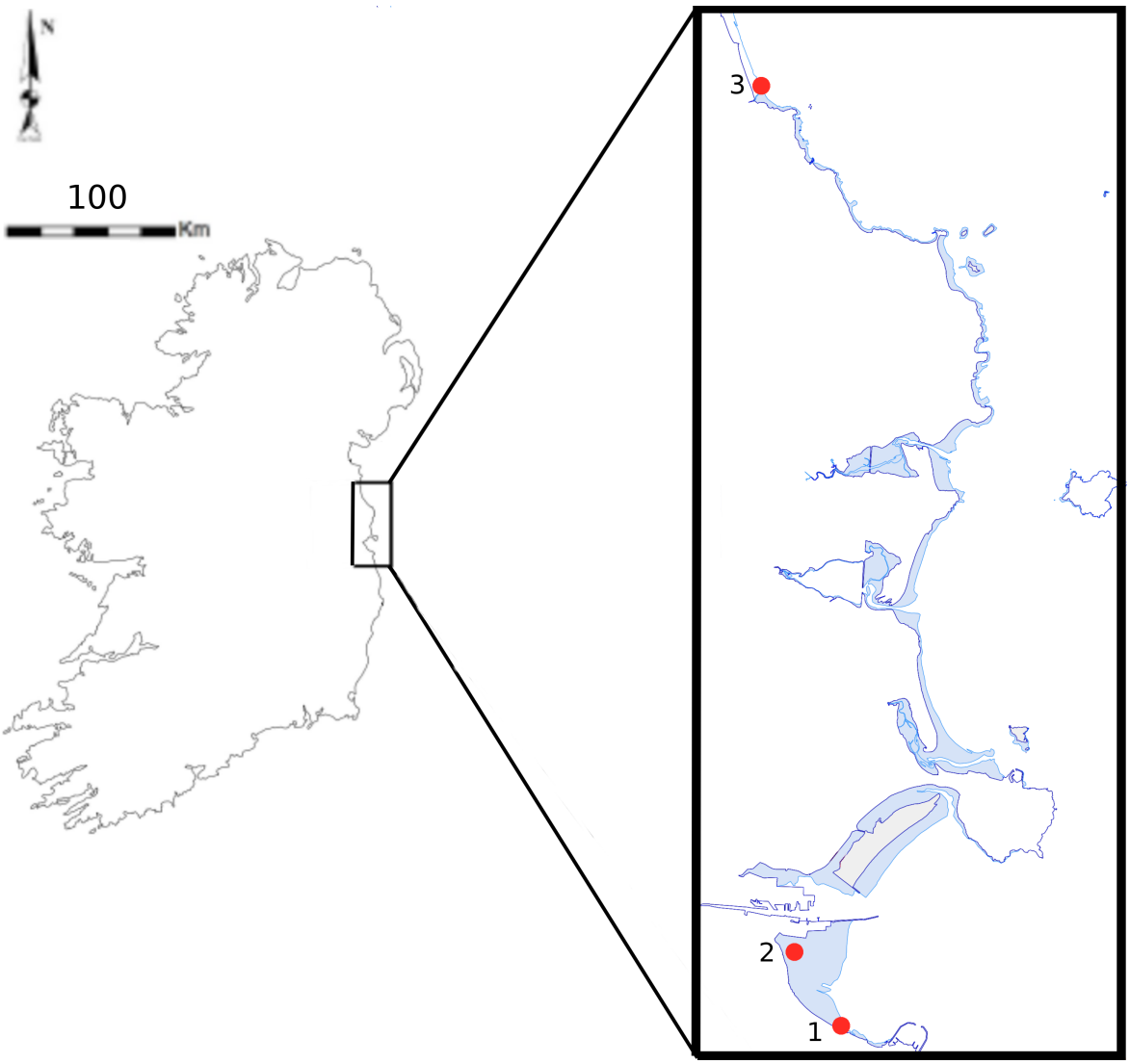


Figure 5.1. Map of Ireland showing the location of the sampling area, with expansion showing sampling locations labelled with red dots: 1: Blackrock, 2: Sandymount, 3: Balbriggan. Map credit Google maps (2017).

5.2 Methods

Algae were provided to bivalves in a stock suspension, with the different sizes of algae forming a variable resource. The food was inert and otherwise homogenous as it consisted of preserved unicellular algae.

5.2.1 Collection of Tellinoids and site selection

Bivalves were collected from sites of known high abundance in Dublin Bay and Gormanstown Beach, Balbriggan, at low tide. *F. fabula* and *M. tenuis* were collected from Blackrock, Dublin

Bay (53°30'33.0" N, 6°17'59.5" W), (Figure 5.1). *S. plana* and *L. balthica* were collected from Sandymount, Dublin Bay (53°32'76.7" N, 6°19'64.8" W), (Figure 5.1) and *D. vittatus* was collected from Balbriggan, North County Dublin (53°63'60.4" N, 6°20'80.2" W), (Figure 5.1). Specimen sizes were chosen to limit size variability, approximately equal sizes for each species were chosen (±10%). Animals were collected in groups of approximately 20, as the experimental set-up allowed for a maximum of 13 animals to be examined at any one time (not counting one control sampling unit). A spade was used to take a sample of the sediment which was subsequently placed in a 1 mm sieve. The sieve was shaken in sea water to separate the sediment from any bivalves present. Bivalves were then removed and transported to the laboratory, in a bucket containing sediment and water from the collection site as soon as possible *i.e.* always within one hour. The experiments were performed during June and July 2012.

5.2.2 Standard laboratory conditions

Prior to, and during, the particle clearance measurement, the bivalves were held under standardised laboratory conditions:

- Clean and uncontaminated seawater, filtered to 0.2 μm (salinity:34).
- Temperature was controlled at a constant 15 °C. 12:12 h (dark:light) light cycle.

5.2.3 Stock solution

The feed given to the bivalves was a high quality stock culture of preserved unicellular algae, derived from a mixture of the commercially available Brightwell Aquatics and Kent Marine brands. The stock was a mixture which was developed to best represent a distribution of sizes of algae from 1.9 μm–20 μm. This stock development would need to be repeated for each subsequent batch of algae purchased, as batches may vary. The stock mixture was achieved by using the mixture of different types of algae at a final cell concentration of 15 000 cells·ml^{-1} or 0.43 mg algal cells ·l^{-1}. The stock developed for this experiment contained 5ml of Phytoplex, 2ml Phytogold-M, 2ml Phytogreen-M 1ml Phytogreen-S in 5L of filtered (0.2 μm) seawater.

Table 5.1 contains the contents of phytoplankton premixes used, all of these mixes were preserved with ascorbic acid and citric acid, meaning the cells used in this experiment were inert.

Table 5.1. Table of algal mixes used in the stock solution showing the brand, species contained and size range

Kent Marine PhytoPlex	*Nannochloropsis* *Tetraselmis* *Isochrysis* sp. *Tahitia*	2–15 μm
Brightwell Aquatics Phytogold-M	*Thalassiosira* sp.	8–20 μm
Brightwell Aquatics PhytoGreen-S	*Nannochloropsis* sp.	1–2 μm
Brightwell Aquatics Phytogreen-M	*Tetraselmis* sp.	10–15 μm

5.2.4 Maintenance and feeding of bivalves prior to experimentation

The animals were placed in a 15 °C constant temperature room and fed with the experimental stock solution for 24 hours before the experiment. They were placed in filtered seawater for two hours before commencing the experiment to prevent feeding and to flush the gut.

If, during the preparation or experimental phase, any gaping or moribund individuals were observed, they were removed as appropriate.

5.2.5 Clearance rate

Standard operating procedure, developed for the clearance rate aspect of the North Sea mussels Scope for Growth study (Widdows *et al.*, 1995a) and ICES method (Widdows and Staff, 2006), were followed as closely as possible with appropriate noted alterations. The standard operating procedures are designed to minimise stress and disturbance of the bivalves during measurement (Widdows *et al.*, 1995a).

An adaptation of the clearance rate experimental method, which measures the removal of suspended particles, was used to determine size preference while suspension feeding. This method was altered by the analysis of the contents of the samples. In this experiment the size composition of the removed particles, rather than the pure clearance rate is examined.

5.2.5.1 Measuring equipment set-up

A Coulter Counter Z2 (Beckman Coulter), was used with a 50 μm aperture and Z2 Accu-Comp v3.01a software. The Coulter Counter uses spherical equivalents to calculate diameters

of particles. As all cells used were spherical/ovoid algae in nature, measurements of their diameters were reliable, and the use of spherical equivalents appropriate. The use of uniform algal body forms in particle selection is important, as otherwise results may not be comparable, for example where elevated reporting of captured *Phaeodactylum tricornotum*, which is known to exist in, and vary between, different morphotypes, was suspected (Bayne *et al.*, 1977). The accuracy and precision of the machine have been determined by Beckman Coulter. The accuracy and precision are determined at the 10,000 count level, averaged from at least twenty replicate determinations (readings), at concentrations below 20% coincidence (Percentage coincidence refers to when particles pass through an aperture simultaneously and are thus incorrectly seen as larger particles (Beckman-Coulter, 2009)). The resultant accuracy parameter is within 1% of a reference counter system. The precision is found to be better than 1% CV (standard deviation expressed as a proportion of the measured value *i.e* at a concentration of 15,000 particles per ml with standard deviation of 300 particle per ml the CV would be 2%) at metered volumes 0.5ml and 1.0ml (Beckman-Coulter, 2009).

The Z2 Coulter Counter (Beckman Coulter) system was filled internally with diluent, which allows conductivity across the aperture membrane. The diluent used was 0.2 μm filtered seawater, as opposed to the freshwater version usually supplied with the counter system, to counter the effects of osmosis between different salinity solutions. Seawater is a conductive electrolyte, so is suitable as a diluent. This diluent replacement method is recommended for marine research applications using the Coulter Counter by Beckman-Coulter (2009). Threshold settings used on the counter system were set to a gain of 512 and a current of 4 mA. Calibration of the Z2 Coulter Counter (Beckman Coulter) with plastic spheres for the 50 μm aperture was completed prior to experiments. The measuring range of an aperture is 2–60% of the aperture diameter, so a 50 μm aperture was chosen for particles between 1.9 μm and 20 μm (Beckman-CoulterCoulter, 2016). As the focus of this investigation was particles 1.9–20 μm the Z2 instrument needed to be run twice for each sample, first to detect particles of 1.9–5.80 μm and then 5.8–21.5 μm with a 0.5ml metering volume, as the machine was not capable of a direct measurement of the entire range 1.9–20 μm.

5.2.5.2 Experimental Set-up

Pyrex beakers (150 ml) of height 90 mm and width 60 mm – sampling units – were used as holding chambers. The holding chambers were set up in a constant temperature room. A schematic diagram of the experimental set up shows one half of the experiment (Figure 5.2).

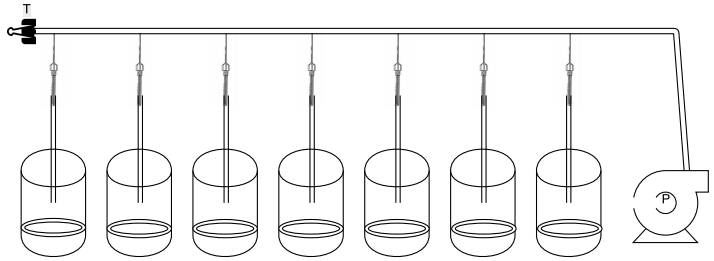


Figure 5.2. Schematic of the experimental set up for particle size preference determination. Sampling units contain a mesh stand on which the bivalve is placed. Air was pumped between the pump (P) and the terminus (T). Mixing could be adjusted up or down by bubbling air via the double straight needle and tube

A length of 4 mm plastic tubing supplied with air from an air pump was set up in a 15 °C constant temperature room, the length of which was long enough to stretch to all sampling units while giving approximately 2 cm between sampling units. Photos of an experiment show the set up (Figure 5.3) and a close up of an animal feeding (Figure 5.4). The tubing was pierced with a double straight needle; with needles 20 mm long, 18 gauge, which were inserted into the tubing allowing a forced circulation of air. Gentle aeration is advised as an alternative where magnetic stirrers are not available (Widdows and Staff, 2006) however needles on their own not only failed to reach liquid after some liquid was removed, but also failed to stir the bottom of the liquid even when the sapling units were full, resulting in settlement of algal cells. After several tests of mixing with varying lengths of tubing added to the needles, 90 mm was chosen as an optimum length. 90 mm length of narrow tube which snugly clasped the needle with no air escaping (sourced from electrical wire) was fitted to the downward facing needle, so that the air would mix the seawater and algae solution and also to ensure that the aeration tube was submerged even when liquid had been removed during samples. The animals were on a mesh raised bed (made of plastic piping and mesh), allowing faeces to settle under the sampling zone. The experimental conditions and the temperature of the constant temperature room, in which experiments were carried out, were checked and recorded daily before each set of measurements.

5.2.5.3 Procedure

Stock suspension of 0.2 μm filtered seawater with 15,000 cells·ml^{-1}, the ideal suspension concentration of algal cells for bivalve feeding (Widdows and Staff, 2006), was made up just

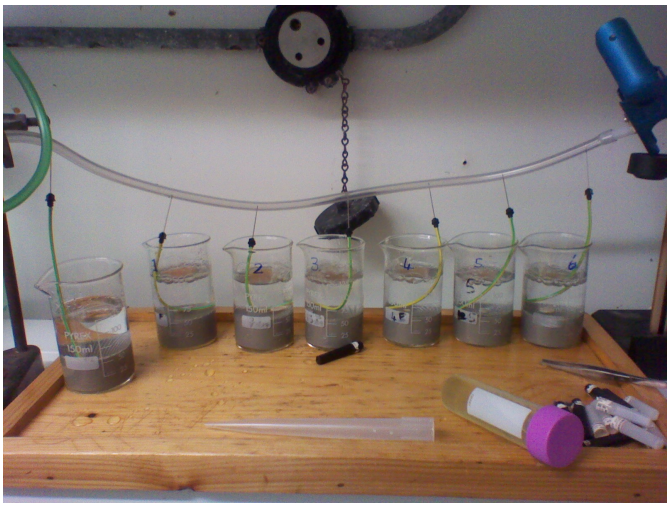


Figure 5.3. Particle size capture efficiency experimental set up

Figure 5.4. Close up of a Tellinoid feeding during a particle size preference experiment

prior to every experimental run. In order to avoid pseudofaecal production and the inhibition of clearance rate, it is best to avoid exceeding a concentration of 15,000 cells $\cdot ml^{-1}$. A 5 litre volumetric flask was used to store the feed "stock suspension" before it was placed in the sampling units for the experiments, the mixture was shaken before each aliquot was removed. 150 ml of solution was added to each sampling unit, and they were left for fifteen minutes to aerate and stabilise. A control was included in all experiments. Individual animals were placed in their respective sampling units using a teaspoon with minimal disturbance to the animal. 10ml of solution was removed from each experimental chamber at each time-point using a 10ml automatic pipette. The samples were read using the Coulter Counter immediately after collection. The glass aperture of the Coulter Counter was rinsed with filtered seawater between readings to prevent cross contamination.

5.2.5.4 Measurement of body sizes

The wet weight of each individual was recorded to ±0.01 mg using a calibrated Mettler Toledo B154-S analytical balance after blotting the animal on tissue paper. Shell length (mm), shell depth (mm) and shell width (mm) were recorded with a Vernier callipers to 0.01 mm for each individual, after the experiment has been completed, to minimise animal disturbance/handling prior to the experiment. Dry weight was established by drying in an oven at 105 ± 5 °C for 24 hours and weighing. Animals were then placed in a furnace at 450°C for 6 hours in order to determine loss on ignition and organic matter content and thus ash free dry weight (mg) (Velasco *et al.*, 2006).

5.2.6 Data analyses

A programme developed to accompany the Coulter Counter to digitise the output was used (Z2 AccuComp software Version 3.01). Data were aggregated from the size categories present in Z2 files generated by the Coulter Counter into larger categories for analysis of relative preferences of each species for particles in each size category. Categories were approximately 0.4 µm wide, varying slightly owing to variation in the underlying Coulter Counter generated category sizes. Statistical data analyses were carried out in R (v3.1.3) (R Core Team, 2016). Data were plotted against time. Outliers, as determined both visually, and by comparison to preceding and following data for an experimental run, with reference to suggested outliers lying outside ±2sd, were removed.

Control data were first examined visually in terms of concentrations and changes in concentration, to remove any clear outliers. They were then regressed in order to determine the average settlement rate for particles of each size, and the standard error of the rate. Where settlement rates were significantly different from zero, these rates were used to correct observed clearance rates in the experimental runs.

For each animal, data were recorded for all particle sizes, for each time-point. Differences between each pair of adjacent time-points were extracted to aid outlier removal. In some instances, there were apparent increases recorded during a time interval in several particle size categories, for one animal. Where one of the time-points involved was an outlier in a linear regression of declining particle count against time, it was deleted from further analysis. Linear regressions of particle count against time were fitted for all particle sizes and all animals, adjusted by any significant decline in the control count. In order to quantify potential extra-treatment effects on particle concentration and size proportions, a concurrent control was included with each experiment, and treated and measured identically to each experimental unit. It was expected that particle counts for every size class in the control unit would remain stable throughout the experiment. The expected level of stability which would allow the analysis of the experimental data, without removal or correction, was not observed in some experimental runs so these were excluded from further analysis. The slopes of the fitted lines were used to determine the particles consumed per minute. Total consumption was calculated by summing the individual particle size-specific consumption rates. Environmental concentrations for each particle size category were taken from concentrations recorded at T_0. Total environmental concentration was the sum of these individual particle size specific concentrations. For the calculation of $\mathbb{E}$ (Ivlev, 1961) for a particle size, the consumed proportion, r_i and environmental proportion, p_i were the consumption rate for that size category divided by total consumption, and particle count for that size category divided by total environmental concentration respectively. $\mathbb{E}$ was then calculated (Equation 5.2).

$$\mathbb{E} = \frac{r_i - p_i}{r_i + p_i} \tag{5.2}$$

5.3 Results

Considerations for low concentration data

Individual particles are often found in natural waters in quantities approximately inversely proportional to particle size (Sheldon and Parsons, 1967; Poulet, 1974). As samples follow a

Poisson distribution, with fewer larger particles, counting accuracy decreases with increasing particle size. When concentrations are sufficiently small, errors can reach or even exceed 100%. For example, when the expected count in a sample is 1, counts of 0 and 1 are equally likely, and counts ≥ 3 are likely to occur with $p > 0.05$. Even at expected count of 10, errors $\geq 60\%$ occur with $p > 0.05$. This imposes an effective limit on the particle size categories which can be included in analyses (Vanderploeg and Scavia, 1979). Universally, the data for particles over 9.5 μm showed such variance that it was too unreliable a result from which to draw any conclusions ($R^2 < 0.1$). The focus of analysis was therefore on particles from 1.9 μm to 9.5 μm.

More efficiently captured particle sizes showed a larger negative coefficient of particle count regressed against time. Any differences between animals, which may have been introduced by animal size, were removed by transforming to $\mathbb{E}$ prior to comparison with other animals.

5.3.1 Experimental results

F. fabula exhibited the strongest preference for larger particles, while *M. tenuis* showed the weakest linear relationship between size and preference of all the species examined. *D. vittatus*, *S. plana* and *L. balthica* all showed a strong positive selection for larger particles, but with particles over (approx) 4.6 μm being equally selected, and no continued increase in capture efficiency, as is seen in *F. fabula* and *M. tenuis*. Capture efficiencies were notable even for *D. vittatus* , but declined (as in *S. plana* and *L. balthica*) slightly in the largest two size categories (8.6–9.5 μm). *D. vittatus* also had the least variability around its particle size capture efficiencies, so these efficiencies varied less from animal to animal. The results graphs are collated in appendix C.

D. vittatus

D. vittatus had relatively little between-animal variation. $\mathbb{E}$ values ranged from a mean of -0.21 for particles below 2.2 μm, representing consumption of 65% of the consumption expected under the assumption of random feeding / equal capture efficiencies, to 0.17 for particles in size category 7.8 μm, representing 1.4 times the expected particle capture rate. Particles were positively selected above 3.8 μm (Figure 5.5).

Overall, particle size accounted for 0.7 of the variance (summed squared deviations). Particles below 3.8 μm were captured with below average efficiency, significantly below all

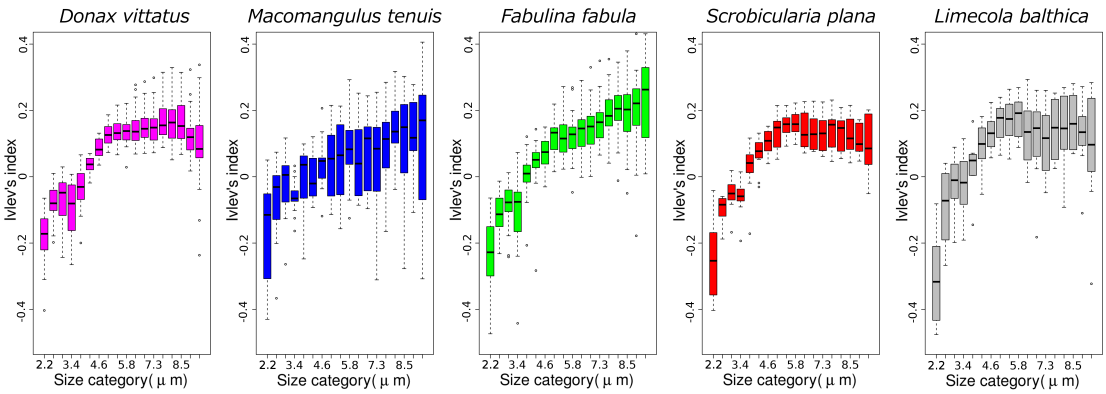


Figure 5.5. Ranges of $\mathbb{E}$ by particle size category, by species. Black bars represent the median, coloured boxes the interquartile range, whiskers (lines extending vertically from the boxes) extend to the full range of the data lying not more than 1.5 times the interquartile range outside of the interquartile range

larger size categories except 3.8–4.2 μm ($\mathbf{p < 0.001}$) which in turn was also indistinguishable only from 4.2–4.6 μm ($\mathbf{p = 0.007}$). The capture efficiency for particles between 4.2 μm and 4.6 μm were statistically indistinguishable from all but two of the larger size categories, while all of the larger size categories were indistinguishable from one another (all pairwise comparisons: Tukey's HSD, $\alpha = 0.05$). The plateau in $\mathbb{E}$ values suggests that *D. vittatus* captures particles from 4.6–9.5 μm and possibly somewhat smaller (though over 4.2 μm) with approximately equal efficiency. This supports the view of suspension feeders as indiscriminate feeders, albeit with a minimum particle size for efficient capture.

M. tenuis

M. tenuis exhibited the greatest degree of variability between individuals i.e. described by height of the boxes and whiskers (Figure 5.5), but the least variability across particle sizes, indicative of broadly even particle capture efficiencies.

Particle size accounted for 0.23 of the overall variance. The efficiency rose steadily from smaller to larger particles, with particles positively selected above 4.2 μm, suggesting that *M. tenuis* did not have a preference for any particular particle size within the range 1.9–9.5 μm, in terms of capture efficiency. Efficiency was significantly higher for particles between 7.8–8.2 μm and between 8.5–9.1 μm than for particles <2.6 μm ($\mathbf{p = 0.02,\ \ p = 0.04}$); and for particles >5 μm than for <2.2 μm ($\mathbf{p = 0.015}$). The above were the only significant differences recorded in *M. tenuis*'s capture efficiencies (Tukey's honest significant difference

(HSD), $\alpha = 0.05$).

F. fabula

F. fabula displayed the strongest relationship between size and $\mathbb{E}$ (Figure 5.5), with regression equation $\mathbb{E} = -0.216 + 0.05 * \text{Size}$, (where size is particle size category) and 0.53 of the variance attributable to size. Particles were positively selected above 3.4 μm. Differences in preference increased consistently with particle size, however there were no significant differences above 4.6 μm. Particles from 7.8–8.2 μm were preferred to those from 4.2–4.6 μm ($\mathbf{p = 0.04}$), Particles from 6.8–9.1 μm were preferred to those <4.2 μm ($\mathbf{p = 0.048}$). Particles >3.8 μm were preferred to those from 3–3.4 μm ($\mathbf{p = 0.008}$). Beyond that, there were a number of differences true for all particles larger or smaller than certain sizes. All particles >5.8 μm were preferred to particles <3.8 μm ($\mathbf{p = 0.04}$), all particles >4.2 μm were preferred to particles <3 μm ($\mathbf{p = 0.003}$) all particles >3.8 μm were preferred to particles <2.6 μm ($\mathbf{p = 0.008}$) all particles >2.2 μm were preferred to particles <2.2 μm ($\mathbf{p = 0.005}$).

S. plana

In *S. plana* 0.69 of variance was attributable to particle size. Particles were positively selected above 3.4 μm (Figure 5.5). Preference increased with particles size, those >4.6 μm were preferred to those <3.4 μm ($\mathbf{p = 0.003}$) and those >3.8 μm preferred to those <2.6 μm ($\mathbf{p = 0.002}$); however particles in the range 5.4–5.8 μm were significantly preferred to particles <3.8 μm ($\mathbf{p = 0.047}$). Particles <2.2 μm were inefficiently captured, being significantly less selected than all other particles >2.2 μm ($\mathbf{p < 0.001}$). There was little variation in preference for particles > 5 μm.

L. balthica

In *L. balthica*, size accounted for 0.6 of variance, with selection again uniform above a minimum size (Figure 5.5). Some size categories 4.6–5.8 μm and 8.2–8.5 μm were significantly favoured over particles < 3.4 μm (**p = 0.008; p = 0.014** respectively), while all particles > 3.8 μm were significantly preferred over those < 2.6 μm (**p = 0.035**). All particles > 2.2 μm were significantly preferred over those < 2.2 μm (**p < 0.001**). Particles were positively selected above 3.4 μm. While preferences for larger particles was more variable in *L. balthica* than for *D. vittatus* , there were no other significant differences.

5.3.2 Variability across species

Ivlevs index $\mathbb{E}$ takes a value of zero for random feeding or no active selection and tends towards plus or minus 1, as a size is respectively preferred (+1) or avoided (-1) (Lechowicz, 1982). If all species were feeding in the same manner, we would expect an ANOVA of $\mathbb{E}$ against size:species to possibly show a net effect of size, but no species or size:species effect on $\mathbb{E}$, *i.e.* if capture efficiencies vary, they vary consistently across species. In a two-factor ANOVA of $\mathbb{E}$ against species and particle size category (size μm), both main effects, size and species, along with the interaction effect, were significant (Table 5.2). Size of particle alone accounts for most variation in the ANOVA, indicating that, across all species, certain sizes were preferred and others less so.

Table 5.2. Analysis of Variance of $\mathbb{E}$ against Size and Species

Asterisks denote significance levels

	Df	Sum Sq	Mean Sq	F value	Pr(> F)
size	17	17.96	1.06	90.19	**<2e-16**
species	4	0.26	0.07	5.58	**0.0002**
size:species	68	1.26	0.019	1.58	**0.0024**
Residuals	1368	16.03	0.0117		

There is a significant size-species interaction, indicating that the degree to which size categories were preferred differed significantly according to the species. As a species which prefers less common particle sizes will have higher $\mathbb{E}$ values on average, there is also a species effect in the model. This effectively represents the tendency of the species to capture less common particle sizes.

5.4 Discussion

The Tellinoidean species examined captured larger particles more efficiently, especially those in the range 4 μm–9 μm. *M. tenuis* , despite having less of a sudden change in positive selection for particles around 4 μm, conforms to the general pattern of more efficiently capturing larger particles, but to a slightly lesser degree than the other species. Despite *F. fabula* having a continuous increase in capture efficiency with size, no significant differences in capture efficiency with particle size were found above 4.6 μm in *F. fabula* or any other species. Particles in the smallest size category (<2.2 μm) were least selected in all species – in the species which tend more to deposit feed (*L. balthica*, *S. plana* and *F. fabula*), particles (<2.2 μm) were significantly less selected than all particles (>2.2 μm).

For particles larger than 9.5 μm the rates of decline in the control and the experimental chambers were extremely variable. For that reason, they were excluded from the analysis. This is possibly on account of the larger particles being less numerous in the mix and being inherently variable owing to the Poisson distribution of their samples, or settling out of solution quickly.

This experiment aimed to measure differences in capture efficiencies with particle size during suspension feeding by offering bivalves an array of sizes of algae. Previous work examining particle size as an axis for niche separation has presented animals with a binary selection of small or large particles of glass microbeads (Taghon, 1992). In order to best determine actual preferences when presented with a range of sizes of algae, as would be present in natural conditions, experimental conditions must seek to emulate the natural conditions as far as possible. While size is the most obvious recordable characteristic for differentiating prey items, recordable characteristics may not match critical characteristics for selection by bivalves and glass microbeads (as used in other studies) may not exhibit the desired characteristics of prey. Organic material which is available to bivalves is diluted with silt, but bivalves are able to preferentially ingest algae (Hawkins *et al.*, 1996, 1998). Preferences for different sizes of glass micro-bead may therefore not accurately reflect preferences of animals under natural prey conditions (Taghon, 1992; Rosa *et al.*, 2015). Bivalves are capable of discriminating between similar sized algae cells (Shumway *et al.*, 1985). This ability to distinguish between different food types could be a means whereby coexisting and potential competing species partition the available food resource (Shumway, 1990), where one bivalve eats one size, the other eats the other size. While there were differences between the Tellinoidean species' relative degrees of preference for different sizes, they did not conform to such

a partitioning of available resources.

5.4.1 Bioaccumulation and ecotoxological implications

The ingestion of microplastics (from the breakdown of plastic debris) can be detrimental to bivalves and their predators or subsequent consumers. Microplastics occur in sizes as small as 4.1 μm (Browne, 2015) or 1 μm–10 μm (Green *et al.*, 2016) which are a viable food size for bivalves (Whyte, 1987), and are often ingested by bivalves (Andrady, 2011), in particular filter feeders (Van Cauwenberghe and Janssen, 2014) some of which can be more indiscriminate in particle capture. Microplastics' large surface area to volume ratio and hydrophobic properties makes them likely to adsorb and concentrate toxic water-borne contaminants from their surroundings, which may dissociate post-ingestion (Wright *et al.*, 2013; Bakir *et al.*, 2012, 2014). Microplastic ingestion can alter the metabolism and burrowing activity of *Arenicola marina* (Green *et al.*, 2016) and could have similar effects in bivalves. There is a gap in knowledge relating to the effects of microplastics on fauna, and the influence of particle size preferences on these effects, therefore the determination of size preferences will aid in understanding potential threat of microplastics on Tellinoids. The comparison of the data derived from this experiment with the size distribution of microplastics in Dublin Bay would prove very useful as an indicative predictor of potential ecotoxicological issues. Species that preferentially select small particles and potentially ingest small microplastics are most at risk owing to the preferential binding of chemicals to smaller particles. This is in essence a corollary to size preference as size preferences have other potential impacts such as the uptake up microplastics and the associated contaminants. Nanoplastics are also of concern and potentially very hazardous to marine inhabitants. Detection methods for nano-plastics in the marine environment are in an early stage of development (Koelmans *et al.*, 2015).

5.4.2 Applicability to natural dietary analysis

Differing preferences for various particle sizes means that some caution is to be used when applying models to species for uptake rates. The results from these experiments suggest that uptake rates vary for size of particle preferentially captured. The tidal cycle and height on the shore could possibly be an explanatory factor in the differing clearance rate measurement results, with *M. tenuis*, living higher up on the shoreline, being less selective than *F. fabula*, owing to the shorter time during which it can effectively suspension-feed.

Widdow's (2006) model of filtration applies a clearance rate in terms of cells per animal per

hour, taking no account of the differences in cells consumed or not consumed for calculation of ingestion levels, meaning it is only appropriate with what it is intended for use *i.e.* a single size of particle such as the flagellate *Isochrysis galbana*. An ideal measure of ingestion preference of natural size ranges would measure particle capture across different size bands, and multiply by a calorific value of a particle in that category rather than assume all particles consumed have a standard average calorific value. The technique used here allows for the adjustment of calorific value based on particle size, providing the potential for a more accurate measure of calorific consumption than the single particle type model.

5.4.3 Size specific capture efficiency

Species with eu-latero-frontal ciliary tracts, such as Tellinoids, retain particles below 7 μm with a much higher efficiency than other species (Mathers, 1974). Particles above 4 μm are typically completely retained in bivalves possessing large latero-frontal cirri (Riisgård, 1988), and this figure is often presented as a threshold for complete particle retention. Results for *D. vittatus*, *S. plana* and *L. balthica* were as expected, with no significant differences in particle capture rates between any two size categories above 4 μm. Size specific capture efficiencies of *M. tenuis* and *F. fabula* followed different patterns however. Capture efficiencies in *M. tenuis* increased gradually, with significant differences only separating particles >5 μm from those <2.2 μm. Significant differences above 4 μm were recorded in *F. fabula* , with the trend of increasing capture efficiency with particle size apparent for the entire size range.

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Chapter 6

Physiological Energetics of Deposivore and Suspensivore Tellinoids from Dublin Bay

Abstract

Scope for growth (SFG), chlorophyll analysis and gut passage time were examined in five littoral species of the Tellinoidea from Dublin Bay, in order ascertain what categorises the energetic niche of each of these bivalves. *Fabulina fabula* had the highest SFG and *Donax vittatus* displayed a negative SFG, the results are consistent with previous studies. The SFG methodology has not been applied to numerous members of the Tellinoidea in tandem before, and is a useful way of making direct energetic comparisons. Gut passage time varied by species with *D. vittatus* having the fastest gut passage time and *Scrobicularia plana* having the longest. Chlorophyll values analysed between faeces from the natural diet compared with faeces produced from a diet of pure *Isochrysis galbana* were inconclusive.

6.1 Introduction

6.1.1 Scope for Growth: A physiological energetic indicator

Scope for growth (SFG) is an integrative physiological indicator using measurements of an organism's physiological variables in order to determine the net energy gain of that organism. It correlates well with and can be used to estimate growth and reproduction (Bayne and

Newell, 1983). Growth rate is an overall measure of performance that is easily interpreted and related to ecological consequences at the population and community levels of organisation (Widdows and Johnson, 1988). In *Mytilus edulis* beds with low biodiversity have low mussel SFG (Crowe *et al.*, 2004). SFG determines the health or fitness of an organism and is used primarily for pollution monitoring programmes owing to pollution negatively affecting SFG in bivalves (Widdows and Staff, 2006). Moderate pollution levels result in typical SFG values in *Mytilus edulis* of between 10 and 16 $Jh^{-1}g^{-1}$, representing coastal areas with an urban influence, such as Dublin Bay. SFG values <5 $Jh^{-1}g^{-1}$, in *M. edulis*, are more typical of areas with high levels of pollution (Widdows *et al.*, 1995a). SFG results for *M. edulis* of 20-25 J $Jh^{-1}g^{-1}$ have been noted in polluted areas (Widdows *et al.*, 1995b). Negative SFG values are indicative of severe stress, the bivalves are in negative energy balance and are using body reserves in order to survive (Widdows *et al.*, 1997). The SFG method was developed and is usually used for suspension feeders, with particular focus on *M. edulis* as an indicator species, but is commonly used in other species. SFG instantaneously provides a measure of the fitness of a bivalve. In the context of this study it is being used to produce a SFG budget for each species for comparative purposes. This in turn can be used to determine the niche to which each belongs in terms of energy requirement. This is used to determine what difference, if any, exists among species in terms of growth. The method is applied in a standard way across all species, following Widdows and Staff's (2006) technique as closely as possible, with some necessary adaptations.

SFG consists of five separate parts, the constituents can be used to determine energy utilisation, without the entire model being used. Portions of what constitutes the SFG method have successfully been used to determine, for example, the feeding rate or respiration rate of an animal, an example of which is where respiration rates were established for *M. tenuis* 0.2 $\mu l \cdot mg^{-1}h^{-1} \approx 0.004J \cdot h^{-1}$) and *F. fabula* ($0.03J \cdot h^{-1}$) (Wilson, 1990). Energy budgets for *Macomangulus tenuis* have been calculated previously, at the population level (expressed $\cdot m^{-2}$). Standing biomass of 0.9-1.3 $g \cdot m^{-2}$ DFW, and production of 9–15 $kJ \cdot m^{-2}$, giving production averaged over the course of a year of 1–1.7 $J \cdot m^{-2}h^{-1}$, equivalent to $0.0011-0.0013J \cdot mg^{-2}h^{-1}$ have been recorded (Trevallion *et al.*, 1970; Trevallion, 1971; Wilson, 1997). Scope for Growth varies throughout the year, with greater production during the summer and loss of condition over the winter. The use of energy budgets, particularly in respect of comparisons across different analyses has been criticised however, owing to each being subject to different limitations of scope, assumptions and conditions (Davies and Hatcher, 1998).

In different climatic and environmental conditions, SFG has been recorded as positive for different portions of the year for Tellinoids such as *Limecola balthica*, with growth only positive from February to early May at the Southern limit of their range (Beukema *et al.*, 1985). Positive growth only commences in June at the Northern limit of the range of *L. balthica*, but continues up to September (Beukema *et al.*, 1985). In the Wadden Sea, *L. balthica* grows only from April–June (Beukema and De Bruin, 1977), which is consistent with its description as growing only at temperatures $0 - 15°C$, subject to food availability and quality (De Wilde (1975) in Beukema and De Bruin, 1977). Growth of *L. balthica* is dependent on a number of interrelated factors however, and the restriction of growth from April to June is not purely based on temperature. When presented with suspended *I. galbana* at various concentrations, where the concentration was within its ideal range for the temperature, *L. balthica* grew, despite a temperature of 20°C (Hummel, 1985). With the recent rapid change in climate conditions and declining stocks of pelagic algae it has been suggested that *L. balthica* may be affected in a negative manner. *L. balthica*'s respiration also increases at high temperatures, with SFG becoming negative (Beukema *et al.*, 2014). The other Tellinoids may be affected in a similar manner.

Mussels which are presented with identical concentrations of particulate organic matter in March and June have been found to have strongly positive SFG in June, but negative SFG in March, owing to reduced ingestion and absorption efficiency (Bayne *et al.*, 1988). It has been suggested that the physiological cost of maintaining a highly efficient digestive system with all digestive enzymes exceeds the benefit this would confer in terms of utilisation of particulate matter, which is only available in short bursts (Bayne *et al.*, 1988). Without such an efficient digestive system, any increase in ingestion, not being matched by an increase in digestion would simply result in a further loss of energy by the animal. The degree to which a littoral bivalve, exposed for several hours per cycle, can compensate for reduced ingestion through increased efficiency is limited, and littoral bivalves have lower assimilated energy than sublittoral bivalves consuming the same suspended material (Bayne *et al.*, 1988). Large-scale studies of another bivalve, *Mytilus galloprovincialis* on the North West Spanish coast in October/November, just before spawning season, found SFG values of 0.01-0.04 $J \cdot \mu g^{-1} \cdot h^{-1}$ (Albentosa *et al.*, 2012).

6.1.2 Analysis of faeces using chlorophyll for dietary quality comparison

The purpose of looking at chlorophyll : phaeophytin ratios in the faeces of bivalves is to estimate the food absorption efficiency of bivalves when fed a homogenous artificial diet of *I. galbana*. Further analysis of faeces produced from a natural diet should then allow the determination of the quality of their natural diets, in terms of ash content. The higher the ash content the lower the organic content and therefore the lower the food quality.

Bivalves consuming a high quality low ash diet should have lower $\frac{Chl\ a}{Phaeo}$ ratios from the natural seston diet, owing to better absorption efficiency and increased conversion of chlorophyll to phaeophytin (Hawkins *et al.*, 1986). Direct comparison across species is limited by each species distinct underlying absorption efficiency for a common standard diet. Measurement of absorption efficiency for a standard *I. galbana* diet allows correction of the natural seston $\frac{Chl\ a}{Phaeo}$ results to take account of this underlying absorption efficiency.

6.1.3 Gut Passage Time: A marker for digestive efficiency

Gut passage time is a standard feeding variable (Stead *et al.*, 2003) and is the observed amount of time taken for the first appearance of dyed faeces to appear after feeding on a marker. Gut retention time or residence time are other ways of describing gut passage time and has been defined as the time necessary for the ingested food to be digested, partly absorbed and partly rejected as faeces (Lucas, 1991). The basic assumption is made that passage rate of potentially digested components equals that of the indigestible marker and that the particle outflows follow 1^{st} order kinetics (Hogan, 1980). The marker must be available at a steady state and then withdrawn. It is important that an inert unabsorbed marker is used. The properties of markers include a material that is inert, non bulky, non toxic, quantitatively recovered (not left in gastro-intestinal tract (GIT) nor absorbed), physically similar or flow at the same rate as substrate, mixes uniformly with the feed, is not affected by GIT secretions, digestion or absorption and is easy to analyse and inexpensive (Kotb and Luckey, 1972). Carmine red was chosen here as the marker, and it has been used previously for determining *Nucula turgida*'s assimilation efficiency (Wilson, 1988). Factors affecting passage time are feeding level, species type, diet composition, the size and form of the foodstuff and the moisture levels of food. It has been found that bivalves which are exposed for part of the tidal cycle do not increase their clearance or ingestion rates to compensate for reduced feeding time (Bayne *et al.*, 1988). They do not suffer a reduction in assimilated energy in proportion to their time exposed, therefore their absorption efficiency increases to partially compensate

(ibid), resulting in an increased gut passage time. Gut passage time is positively correlated with absorption efficiency *(ibid)*, and this, together with the fact that gut throughput is lower for lower ingestion rate, suggests that gut passage time should be inversely correlated with tidal height.

6.1.4 Aims

The aim of this chapter was to culminate the results of three different physiological markers to determine whether any difference exists among the five species of Tellinoids studied.

It was aimed to test whether gut passage time, SFG and chlorophyll absorption efficiency varied among species.

1) H_1: Physiological indices differ between suspension feeders and deposit feeders.

It was expected that suspension feeders would have a higher metabolism due to the effort involved in pumping large quantities of water, and that they would ingest greater quantities of material. It was expected that deposit feeders would have an alternative strategy of low metabolism, increased gut residence time, increased absorption efficiency. A low metabolism has been recently noted as an evolutionarily beneficial adaptation among bivalves (Strotz *et al.*, 2018).

6.2 Methods

6.2.1 Collection of bivalves

Bivalves were collected from known sites of high abundance in Dublin Bay and Gormanstown Beach, Balbriggan, at low tide. *F. fabula* and *M. tenuis* were collected from Blackrock, Dublin Bay (53°30'33.0" N, 6°17'59.5" W). *S. plana* and *L. balthica* were collected from Sandymount, Dublin Bay (53°32'76.7" N, 6°19'64.8" W) and *D. vittatus* was collected from Balbriggan, North County Dublin (53°63'60.4" N, 6°20'80.2" W) (Figure 6.1). Specimen sizes were chosen limit size variability, approximately equal sizes for each species were chosen (±10%). Bivalves were collected in groups of approximately 25 (for SFG, March – May) or 22 (for gut passage time, August – September). A spade was used to take a sample of the sediment which was subsequently placed in a 1mm sieve. The sieve was shaken in sea water to separate the sediment from any bivalves present. Bivalves were then removed and transported to the laboratory, in a bucket containing sediment and water from the collection site as soon as possible *i.e.* always within one hour. Although it would have been interesting to examine

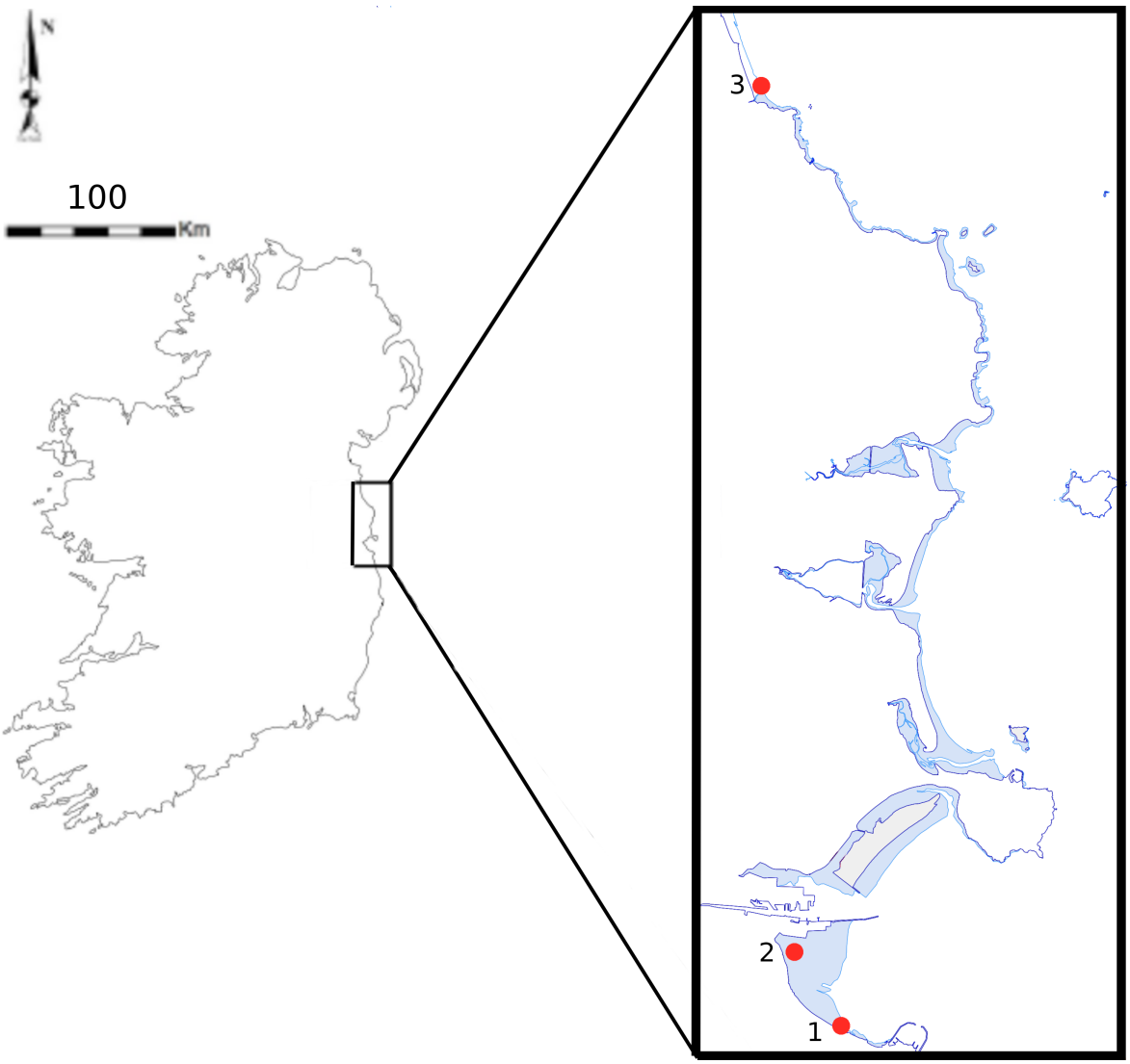

Figure 6.1. Map of Ireland showing the location of the sampling area, with expansion showing bivalve collection sites labelled with red dots. 1: Blackrock, 2: Sandymount, 3: Balbriggan. Map credit Google maps (2017).

size ranges and thus ontogenetic shifts, the specimens available in the field were limited in the range of sizes available and it was decided to focus on limited size ranges.

6.2.2 Scope for Growth

Standard operating procedures, developed for the North Sea mussel study (Widdows *et al.*, 1995a), were followed as closely as possible. These methods are adapted from ICES no 40 (Widdows and Staff, 2006). SFG measurements were performed after a 24 hour recovery period in 0.2 µm filtered sea water (collected from Dublin Bay, Ireland). SFG was performed

on field collected specimens in months March to May 2012. Physiological responses (clearance rate, respiration rate and food absorption efficiency) of mussels were measured under standardised laboratory conditions (i.e. 15°, salinity of 33, and a standard algal ration of *I. galbana*). The standard operating procedures are designed to minimise stress and disturbance of the bivalves during measurement, and to ensure sufficient replication ($n \geq 15$ individuals per site) for the detection of statistically significant differences amongst species (Widdows *et al.*, 1995a).

Groups of bivalves (spares were collected in case of mortality in experimental bivalves) were collected, from locations where they were most abundant in Dublin Bay. Specimens chosen for the experiment were left in a 15°C constant temperature room to acclimatise for 24 hours before the experiment. During this period they were fed *I. galbana* of approximately 15000 cells$\cdot$ml^{-1} (Standard temperature room 15° at 12:12 h (dark:light) light cycle. Feeding rate measurement and respiration measurements were measured within a period of 12 hours after acclimatisation.

Feeding rate measurement The volume of water cleared of particles per animal per hour, or clearance rate, was estimated by measuring the removal of suspended particles from beakers containing 150 ml of aerated seawater with 15000 cells $\cdot$ ml^{-1} of *I. galbana*. This experiment was performed first, after the acclimatisation period was finished.

150ml Pyrex beakers of height 90mm and width 60mm were used as holding chambers. The holding chambers were set up in the cold room. A schematic diagram of the experimental set up shows one half of the experiment (Figure 6.2). A length of 4mm plastic tubing supplied with air from an air pump was set up, the length of which was long enough to stretch to all beakers while giving approximately 2cm between beakers. The tubing was pierced with a double straight needle; with needles 20mm long, 18 gauge, which were inserted into the tubing allowing a forced circulation of air. Gentle aeration is advised as an alternative where magnetic stirrers are not available (Widdows and Staff, 2006). The bivalves were on a mesh raised bed, allowing faeces to settle under the sampling zone (Figure 6.2).

Procedure for feeding rate A 5L volumetric flask of 0.2µm filtered seawater with 15,000 cells$\cdot$ml^{-1} of *I. galbana* was used to store the feed before it was placed in the beakers for the experiments, the mixture was shaken before each aliquot was removed. 15,000 cells $\cdot$ ml^{-1} concentration is the ideal suspension of algal cells for bivalve feeding (Widdows and Staff, 2006). This concentration must not be exceeded in order to avoid pseudofaecal production

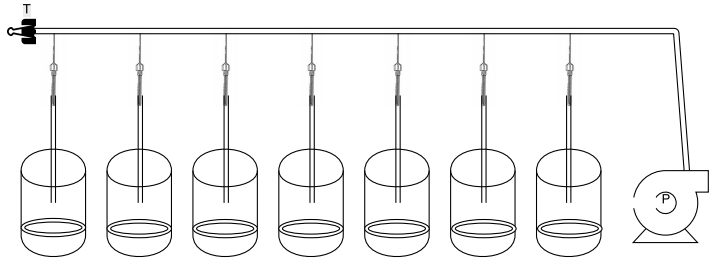

Figure 6.2. Schematic of the experimental set up for the Scope for Growth, beakers contain a mesh stand on which the bivalve is placed. Air was pumped between the pump (P) and the terminus (T). Mixing could be adjusted up or down by bubbling air via the double straight needle and tube

and the inhibition of clearance rate by exceeding the specimen's capacity to ingest filtered particles. A 150 ml aliquot of suspension was added to each beaker which were left for ten minutes to aerate. A control was included in all experiments. Individual bivalves were placed in their respective beakers using a teaspoon with minimal disturbance to the animal. The period of 15 minutes was left to allow the bivalve time to open its shell and resume pumping. After fifteen minutes the sample T0 of 10 ml was removed from each beaker including the control, using an automatic volac pipette with sterile 10ml tips, and pipetted it into a 10ml sample vial with lid (60 x 34mm sample vial for coulter counter with enclosed cap supplied by Sarstedt). The samples were analysed in the Z2 Series Coulter Counter concurrently with the experiment as degradation had been noted in mixtures that were left to sit for periods of time. Samples were quickly shaken by hand, then left to sit for 30 seconds prior to reading with the Coulter Counter, the mean of three counts were taken per sample. Further samples were taken from the experimental beakers and control twenty minutes after T0 namely T1, forty minutes after T0 namely T2, sixty minutes after T0 namely T3, eighty minutes after T0 namely T4. A reading (total particle count per ml) from the screen of the coulter was recorded manually. The coulter counter selectivity settings were adjusted so that particles between 2–8μm were counted, with *I. galbana* size falling within this range.

Respiration measurement Respiration was analysed using a YSI ® 53 Biological Oxygen Monitoring System. A magnetic stirrer was placed in the bottom of the chamber and a mesh on a close fitting plastic ring was placed above the stirrer. Single specimens were placed in a cylindrical chamber (diameter 20 mm), and 5ml of oxygen saturated seawater was added to the chamber. The seawater was filtered to 0.2μm and was autoclaved at 121°C to minimise

microbial activity. A bivalve was then placed on the mesh and a polarographic electrode (YSI reg 5331) was carefully placed into the chamber marking sure that no air remained in the chamber. The chamber was surrounded by flowing 15°C water to maintain a constant temperature. Larger specimens were placed in a larger chamber and the volume of water was noted. Each of the experiments began with the oxygen saturation reading being above 95%. Time and saturation reading were recorded over approximately a 50 minute period. Oxygen consumption rate ($\mu g\ O_2 \cdot h^{-1}$) was calculated for the time period.

All modules of the respiration chamber that were in contact with seawater were cleansed and rinsed with sterile sea water before each run of the experiment. The equipment was sterilised daily to minimise microbial activity. Blank runs were made before each run of experiments to allow for correction of results form background respiration and probe drift. The experimental conditions and the temperature of the respirometry water bath were checked and recorded daily before each set of measurements. Atmospheric pressure was noted and recorded daily.

Food absorption efficiency Food absorption efficiency is determined from loss on ignition (LOI) differences between food and faeces (Widdows and Staff, 2006). The ratio method of Absorption Efficiency = $(F - E)/[(1 - E)F]$ where F = ash-free dry weight:dry weight ratio of food, and E = ash-free dry weight:dry weight ratio of the faeces (Conover, 1966) was used. The ratio represents the efficiency with which organic material is absorbed from a given ingested food material.

20 bivalves of each species were placed in 0.2μm filtered seawater to allow them to purge their digestive systems. Bivalves were left for 12 hours to clear their digestive canal. The bivalves were transferred to a second tank to avoid contamination of the faeces produced while eating *I. galbana*, a flagellate, with faeces relating to the previous natural seston diet. Bivalves were left to feed on I. galbana for 24 hours. Faecal pellets were collected with a 3 ml Pasteur pipette taking care to avoid breaking the pellets. The faeces were transferred into centrifuge tubes (10 ml conical tapered bottoms). The faeces of 10 individuals were pooled to provide sufficient material. The faeces were allowed to settle in tubes, and then most of the seawater was drawn off with a 10ml pipette. 5 ml of 0.5 M ammonium formate was added to the tube and the faeces allowed to settle again. The fluid was then drawn off. This ammonium formate step was repeated twice to remove seawater salts from the faecal samples.

200 ml of algal culture *(I. galbana)* was spun down in a centrifuge to produce an algal

pellet. Three replicates of the algal pellet were made. Seawater was decanted off and the algae rinsed gently with 0.5 M ammonium formate. Centrifugation (ca. 6000 g for 15 minutes) was repeated and washing was completed twice to remove seawater salts from the algal samples.

Algal food samples and faecal samples from each group were placed in separate pre-muffled and pre-weighed crucibles. The samples were dried in an oven at 100±5°C to constant weight (2 d) and dry weights were recorded as soon as possible after cooling in a desiccator. Weights were recorded to ±0.01 mg using a calibrated Mettler Toledo B154-S analytical balance. The samples were then placed in a furnace and were ashed at 450°C for one hour. After the samples were cooled in a desiccator, they were weighed again and the ashed weights were recorded (Widdows and Staff, 2006).

Weighing and measuring specimens The wet weight of each individual was recorded on a Mettler Toledo B154-S analytical balance after blotting the animal on tissue paper. Shell length (mm), shell depth (mm) and shell width (mm) were recorded with a Vernier callipers to 0.01mm for each individual after the experiment has been completed to minimise animal disturbance/handling prior to the experiment. Animals were dissected from their shell and dry weight was established for shell and flesh separately by drying in an oven at 105±5°C for 24 hours and weighing. The resultant measure for the flesh is referred to as dry Flesh weight (DFW) (mg). The samples were then placed in a furnace at 450°C for 6 hours in order to determine loss on ignition and organic matter content and thus ash free dry weight (Velasco *et al.*, 2006).

6.2.3 Assimilation efficiency experiment using chlorophyll (pigment) analysis

Tellinoids were collected from the field and left in 0.2μm filtered seawater for 12 hours. The faeces produced were collected (1mg faeces (≈40 pellets)) and represented faeces produced from the natural diet. The Tellinoids were then left in 0.2μm filtered seawater for a further 12 hours. They were then fed *I. galbana* for 12 hours and the resultant faeces represented faeces produced from that diet. 1 mg faeces (≈40 pellets) were collected and put on filter paper (GFC Whatman). The same procedure was followed for each treatment (faeces derived from natural diet and faeces derived from a diet of I. galbana). The filter paper was folded over and squeezed to take any water out, while making sure no faeces were lost. Each sample was stored in a polypropylene centrifuge tube containing 10 ml of methanol, wrapped in aluminium foil and kept in the fridge at 3°C. A standard procedure for determining chlorophyll in aquatic

environments was used (Standing Committee of Analysts, 1983) including the additional step of acidification to measure phaeophytin (Lorenzen, 1967; Kramer *et al.*, 1994). Acidification causes the loss of a magnesium ion from chlorophyll, converting it to its degradation product, phaeophytin, which has a lower optical density at 665 nm (Lorenzen, 1967; Lichtenthaler, 1987). Phaeophytin was estimated to ensure an accurate determination of chlorophyll levels and as a measure of the condition of algae using the ratio of phaeophytin to chlorophyll (Franson, 1998).

Samples for the determination of chlorophyll were shaken and then removed from their cover of aluminium foil. The lids were loosened and the tubes were placed in a water bath at 65 - 70°C until the methanol boiled for approximately 10 seconds. Boiling for a short period does not degrade chlorophyll but improves the extraction of pigments (Tett *et al.*, 1975). The covering aluminium foil sleeve was then re-placed on each sample, and the samples were allowed to cool to room temperature. After cooling, the filter papers containing the faeces were removed from the tubes. Samples were centrifuged for 8 minutes at 3500 rpm in a centrifuge until the supernatant was clear.

Optical densities of the supernatant were measured against a methanol blank at 665nm and 750nm. A 10ml pasteur pipette was used to transfer 7ml of extract to the 5cm path length cuvette. Absorbance was measured using a UV visible spectrophotometer (Hach®DR5000). The sample absorbance was measured at 665 nm (the chlorophyll peak) and at 750 nm (turbidity correction)(Lorenzen, 1967). Approximately 3 drops of 1M Hydrochloric acid were added to the cuvette to convert chlorophyll to phaeophytin and allowed to react for one minute before the absorbance was measured at 665 nm and 750 nm again. The quantity of acid added does not affect the reduction in absorbance (Lorenzen, 1967). Cuvettes were cleaned with distilled water and methanol between samples.

Chlorophyll and phaeophytin were calculated using absorbance measurements at 665nm and 750nm before and after acidification (Lorenzen, 1967). Constants of $A = 79.95$, $K = 2.43$ were used (Equations 6.1 and 6.2).

$$Chl\ a = \frac{AK(665_o - 665_a)V_{ext}}{V_{sample}L} \tag{6.1}$$

$$Phaeo = \frac{AK(1.7 \cdot 665_a - 665_o)V_{ext}}{V_{sample}L} \tag{6.2}$$

These calculate concentrations in $\mu g \cdot L^{-1}$, which, for 1mg faeces in 10mL, equates to $10ng \cdot mg^{-1}$, or $\times 10ppm$

6.2.4 Gut Passage Time

The method followed that of Wilson (1988) using carmine red as a label. Bivalves were placed in 150ml beakers in 0.2µm filtered sea water containing a mixture of *I. galbana* and carmine red for one hour. The bivalves were then placed in separate 200 ml beakers filled with filtered sea water with no food, where they were observed for time taken for the first appearance of red dyed faeces. Gut clearance time was calculated from feeding until the first pellets containing carmine red appeared. The passage time was compared among species.

6.2.5 Data analysis

All analyses were performed in the statistical package R (3.1.0) (R Core Team, 2016). An ANOVA was carried out on gut passage time data. SFG was computed in excel and comparisons made using an ANOVA in R. Post-hoc tests were used to distinguish pairwise differences following ANOVAs of GPT and SFG. Chlorophyll calculations were computed in Excel (Microsoft). To test whether faster metabolism correlated with a shorter gut passage time, a linear regression model was constructed in R.

6.3 Results

6.3.1 Scope for Growth

The results for SFG, expressed per mg of flesh dry weight, differed significantly with species ($\mathbf{p = 0.01}$, Table 6.1, Table 6.3). *D. vittatus* had slightly negative SFG, while *F. fabula* had a very wide variance in its SFG (Figure 6.3). Post-hoc analysis using Tukey's (1953) HSD found that only *F. fabula* and *S. plana* differed significantly from one another among pairs of species (Table 6.2).

Expressed as annualised biomass production, if the observed values for net production were applicable throughout the year, values (mg$\cdot$ mg^{-1} which is milligrams of production

Table 6.1. Analysis of Variance of Tellinoid Scope for Growth by Species.

	Df	Sum Sq	Mean Sq	F value	Pr($> F$)
Species	4	0.01228	0.0030690	3.5	**0.01**
Residuals	120	0.10523	0.0008769		

Table 6.2. Post-Hoc Tests of Differences in Scope for Growth between Species.

Species 1	Species 2	Difference	Lower	Upper	Adjusted p
M. tenuis	*D. vittatus*	0.020	-0.008	0.047	0.270
F. fabula	*D. vittatus*	0.028	-0.001	0.057	0.060
S. plana	*D. vittatus*	0.002	-0.024	0.027	1.000
L. balthica	*D. vittatus*	0.006	-0.019	0.031	0.960
F. fabula	*M. tenuis*	0.008	-0.018	0.034	0.913
S. plana	*M. tenuis*	-0.018	-0.041	0.004	0.173
L. balthica	*M. tenuis*	-0.014	-0.036	0.008	0.420
S. plana	*F. fabula*	-0.026	-0.051	-0.002	**0.025**
L. balthica	*F. fabula*	-0.022	-0.045	0.002	0.083
L. balthica	*S. plana*	0.005	-0.015	0.024	0.966

Table 6.3. Summary Table of Scope for Growth results.

species	n	mean	sd	ingestion	respiration	Gut Passage	Chl $a(nat)$
D. vittatus	15	-0.001	0.01	0.02	0.02	163	3.03
M. tenuis	22	0.02	0.04	0.05	0.01	394	1.38
F. fabula	18	0.03	0.06	0.22	0.08	319	7.27
S. plana	32	0.0003	0.01	0.009	0.006	444	0.94
L. balthica	38	0.003	0.01	0.008	0.003	211	2.5

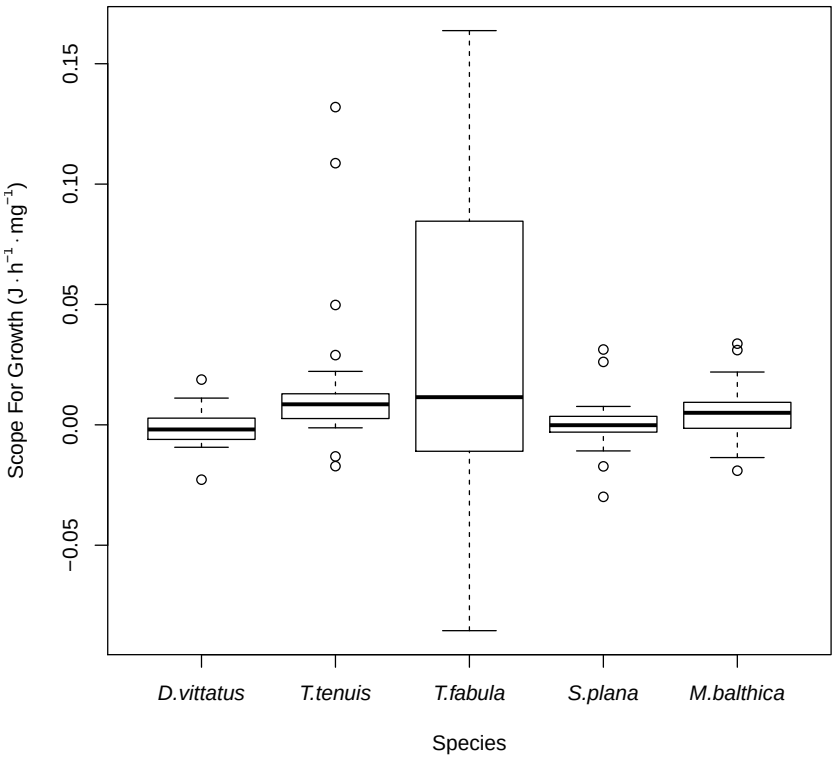

Figure 6.3. Boxplot of Tellinoid Scope for Growth ($Jh^{-1}mg^{-1}$).

annually per milligram of standing biomass) were as follows: *M. tenuis*: 4.18, *F. fabula*: 5.99, *L. balthica*: 0.56, *D. vittatus*: negative −0.29 and *S. plana*: 2.45.

6.3.2 Gut Passage Time

S. plana had the longest gut passage time, taking 444 minutes on average. This was closely followed by *M. tenuis* and then *F. fabula*. *D. vittatus* had the shortest gut passage time. The data were variable, despite results coming from tightly aligned size ranges per species (+/- 10%), all displaying a high standard deviation for gut passage time (Table 6.4.)

Table 6.4. Gut passage time summary statistics (minutes).

species	mean	sd	median	minimum	maximum
D. vittatus	163	170	103	43	777
M. tenuis	394	222	272	144	790
F. fabula	319	130	310	125	537
S. plana	444	207	387	130	790
L. balthica	211	104	190	63	540

There were a small number of outliers in the gut passage time data, and as a result not all of the data were strictly normal. On visual inspection only *D. vittatus* appeared noteworthy, a non-parametric Kruskal-Wallis test was performed (Kruskal-Wallis χ^2: 47.9, **p = 1e-9**). Tukey's (1953) HSD was used for post-hoc discrimination between gut passage time for pairs of species.

While there were significant differences in gut passage time between species (Tables 6.5, 6.6), these were not related to differences in respiration rate, as the correlation coefficient for gut passage time and respiration was negligible ($R^2 = 0.0008$, $p = 0.96$). There was

Table 6.5. Analysis of Variance of Gut Passage Time against Species.

	Df	Sum Sq	Mean Sq	F value	Pr(> F)
Species	4	1480179.6	370044.9	13.16	< **1e-5**
Residuals	126	3543302.05	28121.4		

Table 6.6. Post-Hoc pairwise differences in Gut Passage Time between species using Tukey's HSD.

Species 1	Species 2	Difference	Lower	Upper	Adjusted p
F. fabula	*M. tenuis*	-74	-212	63	0.57
D. vittatus	*M. tenuis*	-230	-367	-94	7e-5
L. balthica	*M. tenuis*	-183	-312	-53	0.01
S. plana	*M. tenuis*	50	-86	187	0.84
D. vittatus	*F. fabula*	-156	-286	-26	0.01
L. balthica	*F. fabula*	-108	-231	15	0.11
S. plana	*F. fabula*	125	-5	255	0.07
L. balthica	*D. vittatus*	48	-74	169	0.8
S. plana	*D. vittatus*	281	152	410	2e-7
S. plana	*L. balthica*	233	111	355	5e-6

similarly no significant relationship to ingestion rate ($R^2 = 0.013,\ p\ =\ 0.86$). Gut passage time may also be an adaptation to the proportion of time spent covered by water or height on the shore. *M. tenuis* were collected for this study from a location in the upper intertidal, covered by water for approximately 40% of the tidal cycle. *F. fabula* on the other hand were collected from close to the spring low water mark, and from channels in the low intertidal which are covered $> 90\%$ of the time. *S. plana* and *L. balthica* were collected from the mid-tidal flats which are covered for 40-50% of the tidal cycle. *D. vittatus* were collected close to the spring low water mark, and were immersed for in excess of 95% of the tidal cycle. There was no significant correlation between height on shore *i.e.* percentage of time spend submerged with the gut passage time results ($R^2 = .298, p\ =\ 0.34$).

6.3.3 Chlorophyll

The results were inconclusive, as they included a very large degree of variance, together with impossible values/contradictions. The values for phaeophytin + chlorophyll were smaller than the values for chlorophyll alone from the faeces produced by two species of bivalve feeding on *I. galbana* (Table 6.7). The concentration of phaeophytin could therefore not be computed, and this, together with the large degree of variance, prevented the use of *I. galbana* for computation of a standard absorption efficiency for each species.

The results from faecal chlorophyll analysis of bivalves taken from their natural environment did not vary to the same degree as those resulting from a standard diet (Table 6.8),

Table 6.7. Chlorophyll, Phaeophytin and $\frac{\text{Chl } a}{\text{Phaeophytin}}$ Ratio for Tellinoids fed on an *I. galbana* diet.

Species	*Chl a*(*ppm*)	*Phaeophytin*(*ppm*)	Ratio
S. plana	410	199.3	2.06
D. vittatus	2397.4	0	N/A
M. tenuis	58.3	167.5	0.34
L. balthica	229.3	110.7	2.07
F. fabula	97.1	0	N/A

Table 6.8. chlorophyll, Phaeophytin and $\frac{\text{Chl } a}{\text{Phaeophytin}}$ Ratio, natural seston diet.

Species	*Chl a*($\times 10$*ppm*)	Phaeophytin($\times 10$*ppm*)	Ratio
S. plana	126.2	91.3	1.38
D. vittatus	3.9	01.6	2.5
M. tenuis	90.7	96.1	0.94
L. balthica	77.7	25.6	3.03
F. fabula	31	04.3	7.27

however in light of the absence of a standard absorption efficiency of chlorophyll for each species, which would have been calculated from chlorophyll results of bivalves ingesting *I. galbana*, no further processing of these results was performed.

6.4 Discussion

Differences in ability to survive and reproduce help explain distributions in the field were examined. Energetic physiological indices are useful in comparing and contrasting animal performance.

6.4.1 Scope for Growth

While Scope for Growth has been used to provide valuable data relating to the health status of *Mytilus edulis* and other large marine bivalves, its use for Tellinoids has been problematic, possibly owing to their small size relative to variability introduced by experimental error. SFG is a method that was developed for suspension feeders and inherently measures SFG while suspension feeding, the use of sediment in chambers would not be possible. Trevallion (1971) calculated net annual productivity for a standard *M. tenuis* which was less than a sixth of that which would be expected in order to account for the somatic growth of the bivalves. Hughes (1970a) reports a net annual energy gain ($\frac{Production}{Biomass}$) of 63% for *S. plana*, far in excess of what has been recorded in this study, but far less than was recorded for *F. fabula*, *M. tenuis*, while *D. vittatus* experienced negative growth.

Taking the calculated figures, *F. fabula* have an advantage in potential competitive ability in terms of their SFG, however the extremely high value suggests that the small body size made it susceptible to inaccurate readings. The negative result for *D. vittatus* may be a result of the animal being very active and respiring at a higher rate than the other bivalves (showing approximately twice the respiration rate of *M. tenuis* in this investigation), or owing to a lack of suitable quantities and quality of food availability in the clearance experiment. *D. vittatus* may normally ingest particles smaller than *I. galbana* on offer during this SFG experiment. It also had the highest metabolism, at 0.02 $J \cdot mg^{-1}h^{-1}$, apart from *F. fabula*, whose readings were suspect owing to the small size of the specimens. *D. vittatus* may therefore simply have depleted all the resources available in the experiment in the early stages. Interestingly the gut passage time of *D. vittatus* is the shortest, suggesting a very high throughput and metabolism of ingested food, which is consistent with the negative SFG result. The mode of feeding can affect bioenergetics, as certain types of feeding are more energy intensive than others and the amount of energy spent by the gill drawing through food is affected by the type of feeding behaviour. *D. vittatus*'s high metabolic rate can account for higher energy expenditure than the other species, and is consistent with previous findings (Ansell and Sivadas, 1973) (other metabolic rates). *D. vittatus* recorded a negative SFG, but zero was

within the 95% confidence interval for SFG for *D. vittatus*, *S. plana* and *L. balthica*. SFG has been recorded as positive for only a portion of the year for Tellinoids such as *L. balthica* (Beukema *et al.*, 1985), so for much of the year the Tellinoids have near-zero or negative scope for growth. The SFG recorded for the Tellinoids of Dublin Bay represents a snapshot of their physiological condition in Spring, and their ability to grow in conditions of 15,000 cells·ml *I. galbana* at a temperature of 15°C.

The utility of energy budgets and physiological indicators such as SFG has been questioned (Davies and Hatcher, 1998). They are most frequently used for larger commercial shellfish species such as *Mytilus edulis*, partly owing to the commercial value of the results. They also have large clearance rates and experiments using such species consequently suffer limited sensitivity to small fluctuations in particle suspension concentration or oxygen tension. They are also of value in estimating the biological and ecological quality of the habitat (Crowe *et al.*, 2004), however their utility in this regard is limited by animal size, with values for small species such as *F. fabula* being too erratic to be of practical use.

6.4.2 Gut Passage Time

Gut-clearance time is related to the food intake and the assimilation efficiency of a bivalve (Bayne *et al.*, 1988). The gut-clearance time determined here used carmine red inert particle mixed with *I. galbana* and could differ from other markers owing to digestibility differences. It has been noted that diatoms may remain longer than suggested, as there are high numbers observed in sections of the stomach (Hylleberg and Gallucci, 1975). However the use of the flagellate *I. galbana*, which was used here, has not been noted to do likewise. Previously a gut-clearance time of 9 h (540 minutes) was found for *Macoma nasuta*, 11 h (660 minutes) found for *S. plana* at the same temperature (12°C; Hughes, 1969), results which are longer than what was found here. Perhaps the higher temperature of 15°C could account for some of the difference in results, as assuming $Q_{10} = 2$, the results herein would suggest a gut passage time of 547 minutes at 12°C for *S. plana* (Hughes, 1969). (Q_{10} is a standard parameter of reactions which increase exponentially in rate with increasing temperature. It represents the proportional increase in reaction rate observed for a 10°C increase in temperature). No overall interspecific relationship emerged between gut passage time and respiration rate or ingestion rate.

No significant relationship was found between percentage of time spent submerged (height on the shore) with gut passage time. This was interesting, as bivalves that spend more

time exposed would be expected to have a slower gut passage time than the ones that are near-continuously immersed. This is because bivalves with a poorer food supply increase absorption efficiency to compensate, and absorption efficiency is correlated with gut passage time, which cannot be adjusted at the time-scale of the tidal cycle (Bayne *et al.*, 1988).

Correlations between feeding mode and faecal pellet form are pronounced in the Bivalvia (Arakawa, 1971); however no comparison with particle size capture efficiencies or dietary analysis has so far been carried out. The lack of information on the functional relationship of these characteristics means additional clarity could be provided on the feeding biology of these species. The pellets of Donacidae are plain rod shaped, those of Macominae discoid shaped, most other Tellinidae produce ovoid shaped pellets, while the Semelidae may have ovoid, discoid or ellipsoid pellets (Arakawa, 1971).

6.4.3 Chlorophyll analysis

The chlorophyll analysis should have provided some insight into the quality of the Tellinoideans' diets in their natural habitats. More degraded chlorophyll in faecal pellets is typically indicative of a more thorough digestive process and higher assimilation efficiency. The variability of the results of analysis following controlled feeding however, which acted as a level of control, mean that these results were inconclusive. Problems with pre- and post-acidification spectrophotometry yielding impossible or unbelievable results are a known phenomenon in chlorophyll analysis (Moed and Hallegraeff, 1978) and may have contributed to the inconsistent results found here. Recently chlorophyll has been measured directly in the field using hand held meters (Osmond and Park, 2002) and these could possibly be used directly in the lab if phaeophytin comparisons are not required, eliminating the processing steps involved with spectroscopic analysis. Use of a fluorescence microplate reader would be a preferable method to traditional spectrography methods, as less processing of samples is required (Mandalakis *et al.*, 2017)

Chapter 7

Conclusions

An aim of this thesis was to determine where the littoral Tellinoids are found in relation to each other and environmental variables in Dublin Bay. While scattered individuals of some Tellinoid species are found throughout the bay, each Tellinoid species is found at highest abundances in a subset of the Dublin Bay environment. For each species, this environment, where it is found in the highest abundances, or constitutes the greatest proportion of bivalve biomass, is considered to be characteristic of that species. The characteristic environmental conditions associated with each Tellinoid were established (Table 2.1 on page 38).

A further aim was to determine the P:G of Tellinoids from Dublin Bay in order to better define feeding type. In Chapter 3, the P:G of *D. vittatus*, *M. tenuis* , *T. fabula*, *S. plana* and *L. balthica* were found to be 0.5, 0.78, 1.31, 1.38 and 4.12 respectively (Table 3.1, page 68). While the differences in capture efficiencies across species were not as striking as hypothesised, it is notable that *D. vittatus* had effectively equal capture efficiency above 4.2μm, and *M. tenuis* had the most even distribution of efficiencies, while *S. plana* and *L. balthica* , deposivores, had a small peak in capture efficiency at just over 5μm.

The third aim was to establish niche width in terms of particle size using dietary analysis and particle size ingestion analysis. While the Tellinoidean species examined were found to preferentially capture larger particles, especially those in the range 4–9μm (Chapter 5), evidence from their natural diet suggests that smaller particles, owing to their presence in greater numbers, form a vitally important part of the diet of, particularly, *D. vittatus*, but also *F. fabula*, *S. plana* and to a lesser extent, *M. tenuis*. The relatively small proportion of picoplankton found on the crystalline style of *L. balthica* suggests that the picoplankton is not important in the diet of *L. balthica*. Interestingly, there is a high dependence in general

on picoplankton, and any changes in plankton composition towards larger particles would severely affect 4 species of littoral Tellinoidea in the bay. There is no correlation between efficiently captured particle size and the plankton sizes found on the crystalline style, which is surprising. Although it could be assumed that the Irish Sea provided a homogenous feedstock to all the sites where bivalves were collected for the dietary analysis study, there could of course be spatial variation. This would result in different feedstock being available to different species at different locations and may account for this difference. *L. balthica*, particularly found to be deposit feeding, may also be picking up larger particles on the water sediment interface.

The final aim was to determine bioenergetic and physiological indices for the littoral Tellinoidea in Dublin Bay. SFG, chlorophyll analysis and GPT were established, defining energetic niche of each of these bivalves. *F. fabula* had the highest SFG and *D. vittatus* displayed a slight negative SFG. The results are consistent with ranges of SFG in spring reported by previous studies. GPT varied by species with *D. vittatus* having the shortest GPT and *S. plana* having the longest. An analysis of chlorophyll values between faeces from the natural diet and faeces produced from a diet of pure *Isochrysis galbana* was inconclusive.

An overview of the findings from this work, including the above, are presented collated (Table 7.1). P:G measurements vary among species, including a wider than expected variance between *S. plana* and *L. balthica*, both commonly assumed to be deposit feeders, elucidating a specialisation of their feeding modes in Dublin Bay as a possible means of them avoiding competition. Crystalline style analysis provided an indication of the size and shape of the particles ingested in the field and supported the distinction above between *S. plana* and *L. balthica*. Physiological energetics revealed that the SFG of *D. vittatus* was negative while the SFG of all other species was positive, possibly explaining its low abundance in Dublin Bay. Its growing season in Dublin may however occur later in the year than that of the other Tellinoids, as it has been known to occur in Dublin Bay in moderately high densities in some years (Wilson, pers. comm.). The previously noted epidemic mortality of *D. vittatus* , albeit because of food restriction, owing to metabolic stress (Ansell and Sivadas, 1973) because of its high oxygen consumption (Ansell, 1973), may be being intermittently caused by another factor in Dublin Bay. In Gormanstown Beach, Balbriggan, where *D. vittatus* was found, there were no *S. plana*, *L. balthica* or *F. fabula*, and the geography is an open coastline rather than a semi-enclosed bay. Gormanstown Beach, Balbriggan would be subject to different food cycles and flow dynamics than Dublin Bay, changing the competition dynamics. In terms of

sediment type and tidal height, *D. vittatus* would be in potential competition with *F. fabula*, and two individuals were found alongside *F. fabula*, however *F. fabula*, which had high SFG, appears to be more successful within the Bay.

It was hypothesised that Tellinoid deposivores prefer particles within a narrower size range than suspensivores. This was not found to be the case for the littoral Tellinoidea of Dublin Bay. No narrow range of particles was selected by any Tellinoid species.

A further hypothesis was that suspensivores' niche width is greater than that of deposivores. *M. tenuis*, classified here in Dublin Bay as a suspensivore, was a generalist with the broadest realised niche, supporting the proposition. *D. vittatus*, the other suspensivore, and *F. fabula*, with mixed feeding mode, were, however, more restricted in their realised niches than *S. plana*, more of a deposivore than *F. fabula*, and *L. balthica*, a deposivore.

The final hypothesis was that suspensivore communities have greater dominance than deposivore communities. This implies greater evenness (inverse of dominance) in deposivore communities. This was supported by comparison of Pielou's (1966) indices for bivalves in locations examined. Locations with high abundances of Tellinoid suspensivores had much lower evenness index values than locations with high abundances of Tellinoid deposivores.

Key aspects of the behavioural and physiological characterisation of Tellinoids are their feeding mode and energetics. The Tellinoid species are ranked according to their apparent tendency to deposit or suspension feed based on the characteristics associated with feeding mode. The outcome of the standard physiological parameters Scope for Growth and Gut Passage Time are also ranked (Table 7.2). In terms of places, *D. vittatus* comes out first on two of the measures associated with feeding mode, and equal second on the third. This validates the view of *D. vittatus* as an obligate suspensivore. Interestingly, it also has the fastest gut passage time. *L. balthica* is placed last in terms of suspensivory for P:G, as it had the largest ratio; and style contents, as it had the largest particles. *L. balthica* had the second fastest GPT after *D. vittatus*, indicating that this measure is not necessarily associated with feeding mode in Tellinoid species. There is similarly no relationship between SFG while suspension feeding and feeding mode.

Competition between species is likely to be more intense where the species occupy overlapping niches. Niche descriptions have multiple dimensions, and overlap between pairs of species on some of these dimensions has also been recorded, such as P:G (Table 7.3). Deposit feeders are thought to have narrower niches than suspensivores (Levinton, 1971), with P:G

Table 7.1. Summary of results for each Tellinoid species. Feeding Mode (Lit) is the accepted classification of each species in the literature (S=Suspensivore; D=Deposivore). Style size and shape refer to the most common size and shape of algae respectively found on the Crystalline Style following a natural diet (Explanation Figure 4.1, page 93; Figure 4.5, page 93); CE point refers to the size above which particles are captured at greater concentration than in the environment, SFG is expressed in annualised production per unit biomass ($mg \cdot mg^{-1}$), Gut Passage Time is in minutes, and $\frac{\text{Chl } a}{\text{Phaeophytin}}$ is the ratio of Chl *a* and Phaeophytin found in the faeces of Tellinoids consuming a natural diet.

Species	*L. balthica*	*S. plana*	*F. fabula*	*M. tenuis*	*D. vittatus*
Feeding Mode (Lit)	S/D	S/D	S/D	S/D	S
P:G	4.12	1.38	1.31	0.78	0.5
Feeding Mode (This work)	D	S/D	S/D	S	S
Style Size	Nano	Pico	Small Nano	Small Nano	Pico
Style Shape	A	A	A/E	E	A
CE point	>3.4μm	>3.4μm	>3.4μm	>4.2μm	>3.8μm
SFG	0.56	0.06	5.99	4.18	-0.29
Gut Passage Time	190	387	310	272	103
$\frac{\text{Chl } a}{\text{Phaeophytin}}$ (Natural)	3.03	1.38	7.27	0.94	2.5

an indication of feeding mode (Wilson *et al.*, 1990; Compton *et al.*, 2008). P:G can also be thought of as a niche dimension in itself, and as such, the difference between *L. balthica* and *S. plana* separates their niches to reduce competition. In this dimension, potential competition between *F. fabula* and *S. plana* would be highest, as they had very similar P:G.

Particle size capture efficiencies were significantly different between species, but the overall pattern of more efficient capture over ≈4μm held across species. *S. plana* and *L. balthica* are very similar in terms of capture efficiency, while *M. tenuis* is the most different from those species. *F. fabula* and *M. tenuis* both consistently capture larger particles more efficiently, but the strength of the relationship between particle size and capture efficiency is stronger for *F. fabula* (Figure C.2, page 197; Figure C.3, page 197), therefore if the composition of the seston were to change to include a greater proportion of larger particles, it is possible that the relative abundances in the field of *F. fabula* and *M. tenuis* could change, favouring *F. fabula* where their ranges overlap (Table 7.4).

In terms of crystalline style contents, *L. balthica* is very different to the other species, with *M. tenuis* being the closest to *L. balthica*. *D. vittatus* is at the other extreme, and would

Table 7.2. Ranking of species on suspensivore (1) to deposivore (5) feeding gradient according to palp:gill ratio (P:G), Style Contents, Particle capture efficiencies; Ranking of SFG (1 highest) and GPT (1 quickest).

Species	Palp:Gill	Style Contents	Capture Eff.	SFG	GPT
D. vittatus	1	1	2=	5	1
M. tenuis	2	4	1	2	3
F. fabula	3	2	5	1	4
S. plana	4	3	2=	4	5
L. balthica	5	5	2=	3	2

be potentially competing with *F. fabula* and *S. plana* (Table 7.5)

The environmental characteristics in which species are found are an important component of their niche, and the degree of overlap of physical environmental characteristics for each pair of species is also recorded (Table 7.6). *F. fabula* and *S. plana* would experience medium to high potential competition based on the niche characteristics P:G, particle size capture efficiency and crystalline style contents if they co-occurred. The fact that their ranges do not overlap in Dublin Bay, is possibly owing to the fact that their competition potential based on environmental characteristics is low, meaning that in reality there is very little competition between them. *S. plana* and *L. balthica* have a low degree of potential competition based on P:G and crystalline style contents, but their potential for competition is high, and they are found sympatrically, so the low degree of potential competition in the two measures may be related to niche division through ecophenotypic plasticity, with *S. plana* suspension feeding more, and *L. balthica* being a deposivore in Dublin Bay, despite the ability of both species to use both feeding modes.

Table 7.3. Degree of potential competition based on palp:gill area ratio. H=high, M=medium, L=low

Species	*M. tenuis*	*F. fabula*	*S. plana*	*L. balthica*
D. vittatus	M	L	L	L
M. tenuis		M	M	L
F. fabula			H	L
S. plana				L

Table 7.4. Degree of potential competition based on particle size capture efficiencies. H=high, M=medium, L=low

Species	*M. tenuis*	*F. fabula*	*S. plana*	*L. balthica*
D. vittatus	M	M	M	M
M. tenuis		M	L	L
F. fabula			M	M
S. plana				H

Table 7.5. Degree of potential competition based on crystalline style contents. H=high, M=medium, L=low

Species	*M. tenuis*	*F. fabula*	*S. plana*	*L. balthica*
D. vittatus	L	H	H	L
M. tenuis		M	M	M
F. fabula			H	L
S. plana				L

Table 7.6. Potential for competition based on environmental characteristics. H=high, M=medium, L=low

Species	*M. tenuis*	*F. fabula*	*S. plana*	*L. balthica*
D. vittatus	H	H	L	L
M. tenuis		H	L	L
F. fabula			L	L
S. plana				H

Competition between the Tellinoidea is evident, there appears to be a greater reduction of *M. tenuis* below the LWM in the presence of *F. fabula* than in the presence of *D. vittatus*. Despite surviving in silty environments, *M. tenuis* is perhaps less suited to the silty habitats typical of *L. balthica* and *S. plana*. The types of competition experienced by deposit and suspension feeders differs and those that engage in both modes of feeding behaviours will experience both types of potential competition to greater or lesser degrees. Their classification in terms of deposit/suspension feeding mode should suggest the forms of competition which are most appropriate for a competition study including that species. Where a species, which may deposit- or suspension-feed, co-exists with another species with similar feeding behaviour, one or more of the species may differentiate their feeding mode as a form of niche specialisation to minimise potential interspecific competition. Where two cohorts of the same species (*L. balthica*) had the same feeding behaviour, the growth of the juveniles was depressed relative to a population where adults had a different feeding mode (Olafsson, 1989). This suggests that the differentiation of *S. plana* and *L. balthica* in terms of P:G ratio in Dublin Bay may be a local phenomenon, or one which occurs where they co-exist, rather than their default behaviours. Size effects could occur where small specimens with small gills have low throughput of material, which increases as they grow, thus more competition for interaction with other individuals and direct competition is to be expected.

The acquisition of food is dependent on species' adaptive morphology and behaviour in feeding by suspension or deposit feeding modes (Stead *et al.*, 2002). Suspension feeding communities are more vulnerable to being wiped out by catastrophic events than deposit feeding communities (Levinton, 1972; Sheehan and Hansen, 1986; Rhodes and Thayer, 1991), therefore the results of P:G comparison suggest that *S. plana*'s existence may be more vulnerable, relative to *L. balthica* in Dublin bay than would be expected by inference from their relative

abundances (Chapter 2). The reason that suspension feeders are more susceptible to population collapse is that anything which causes a drastic reduction in phytoplankton production cuts off their food supply, while deposivores have an effective reservoir of material which can be consumed during such events (Sheehan and Hansen, 1986; Rhodes and Thayer, 1991).

Deposivores and suspensivores often occupy effectively mutually exclusive areas, owing to the tendency of deposivores to alter the sediment structure in a way that makes it less suitable for suspensivores (Rhoads and Young, 1970). The communities of bivalves were dominated in Blackrock and Gormanstown Beach, Balbriggan by suspension feeding Tellinoids, in coarse clean sand. The communities in Sandymount and Bull Island, while including populations of the suspensivore *Cerastoderma edule*, included a large proportion of deposit feeders. As a consequence of Levinton's (1971) hypothesis, it was expected that dominance would be higher in suspensivore communities, and therefore evenness higher in deposivore communities. The suspensivore bivalve communities had Pielou's (1966) evenness of $0.18-0.36$, while the bivalve communities with deposivores had evenness of $0.67-0.71$. Shannon's (1948) index of diversity values for bivalves ranged from $0.38-0.50$ in the suspensivore communities to $1.19-1.27$ in the communities with deposivores. These results are consistent with the predicted consequences of Levinton's (1971) hypothesis.

Several physiological and behavioural characteristics of Tellinoids are correlated with environmental characteristics and with one another. The characteristics of the Dublin Bay Tellinoids and their environments were analysed for such correlations (Figure 7.1). Scope for growth, gut passage time and dietary analysis reveal the flow of energy through ecosystems. As SFG correlates with measures of biodiversity in communities (Crowe *et al.*, 2004), parameters which correlate with SFG may provide some indication of ecosystem health. Taking SFG measurements throughout the year would give a better understanding of species and ecosystem health, as limited conclusions can be elucidated from a snapshot in the spring.

Strong correlations were seen between P:G ratio and silt content, consistent with deposit feeders normally being found in high silt environments (Figure 7.1). The P:G classification (Chapter 3) considers *F. fabula* more of a deposit feeder than *M. tenuis*, despite the latter here tolerating greater levels of mud. P:G also correlated positively with size of particles in the natural diet found on the crystalline style, perhaps indicating that deposit feeders ingest larger particles. *M. tenuis*, the most abundant and widespread Tellinoid, showed the greatest potential in terms of competitive ability, while *D. vittatus* showed the least. *L. balthica* and *S. plana* may compete for shared resources, being found in the same environments, sharing

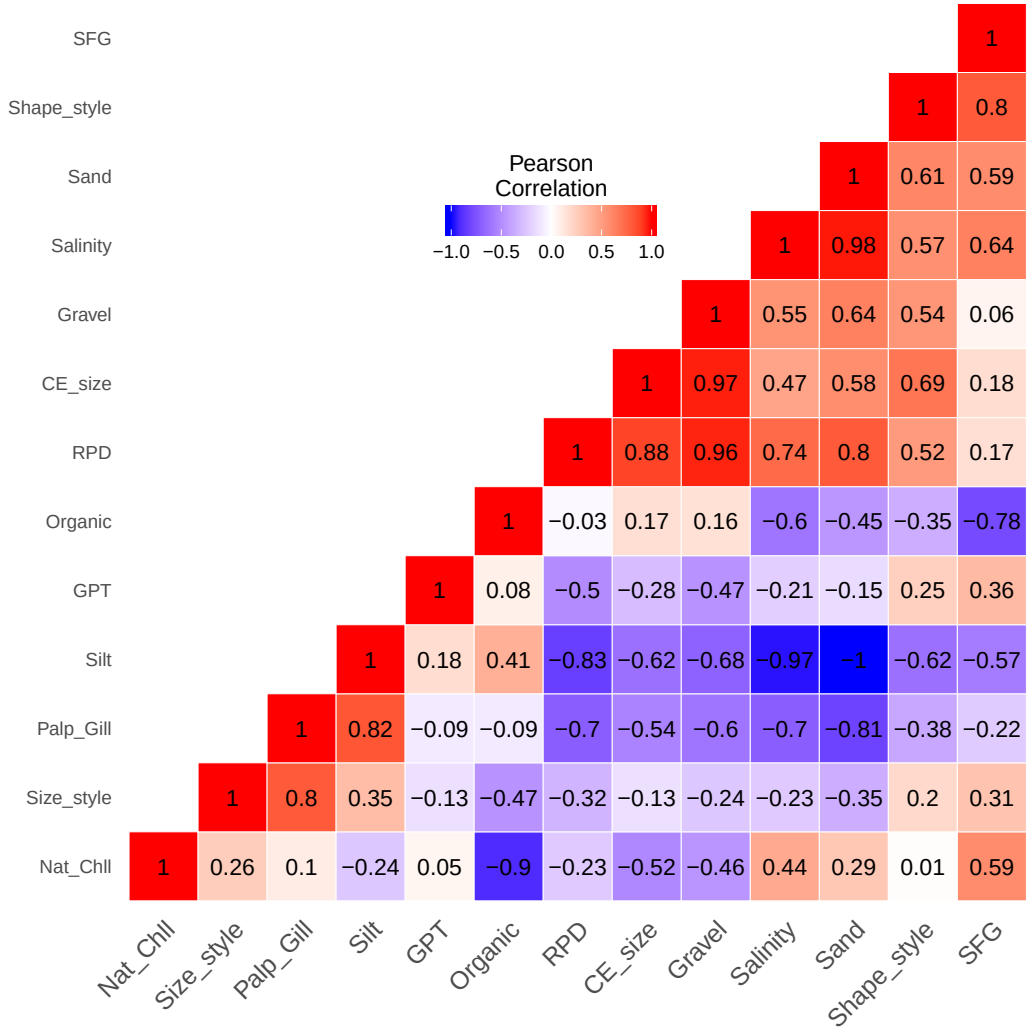

Figure 7.1. Matrix of correlations between environmental and physiological variables. Environmental and physiological variables are explained in legends of table 2.1 on page 38 and table 7.1 on page 148 respectively.

a feeding mode and capturing sizes of plankton with similar efficiency, but with *S. plana* ingesting smaller particles in its natural diet. *F. fabula* and *D. vittatus* are also found in similar environments to each other, mostly near the Low Water Mark in clean sand, consuming small particles in the natural environment, but preferring larger particles, and both being subject to increasing competition with *M. tenuis* towards the mid-shore. Interestingly, they do not co-occur to a large degree. *M. tenuis* is found in all environments, has high Scope For Growth, and is much more successful where *F. fabula* and *D. vittatus* also occur.

There is, however, no direct relationship between the P:G (Chapter 3) and this point where captured, *i.e.* dietary proportions exceed environmental proportions, i.e. $\mathbb{E} > 0$ (Table 7.7).

Table 7.7. Zero-point of $\mathbb{E}$ against Size by Species. The zero point is where the graph of $\mathbb{E}$ crosses the x axis, i.e. the particle size above which there is positive selection.

Species	Zero Point	P:G Ratio
M. tenuis	4.202	0.78
D. vittatus	3.807	0.5
T. fabula	3.411	1.31
S. plana	3.411	1.38
L. balthica	3.411	4.12

In terms of particle size capture efficiencies it was expected that suspension feeders would have a wider variety of particle sizes than deposit feeders (Levinton, 1972), however no significant relationship was found between feeding mode and dietary width, either with conventional classifications or with P:G area ratio (Chapter 3). The more naturally suspension-feeding (according to P:G) species are distinguished from the more deposit feeding species, but there is no clear relationship to P:G ratio (Table 7.7). *D. vittatus* had overwhelmingly picoplankton contained on its crystalline style and this may have had an effect on the clearance rate component of SFG, where *D. vittatus* didn't particularly select the size ≈4μm of food given. The sizes of particle found on the crystalline styles of bivalves indicate that ingestion of microplastics possible with a potential of microplastics having a negative effect on all of the species examined, although no microplastics were noted on the crystalline styles of the Tellinoids examined. As microplastics of size of 4.1μm (Browne, 2015) or 1–10μm (Green *et al.*, 2016) are common, they are a potential food size for bivalves (Whyte, 1987), and have been found

to be ingested by bivalves (Andrady, 2011), in particular filter feeders (Van Cauwenberghe and Janssen, 2014). Microplastic ingestion can, owing to the toxicity associated with them, cause altered metabolism and burrowing function (Wright *et al.*, 2013; Bakir *et al.*, 2012, 2014; Green *et al.*, 2016).

A clear example of resource partitioning by particle size within a single feeding mode was not in evidence among the Dublin Bay littoral Tellinoidea, however, the increased divergent specialisation of *L. balthica* towards deposit feeding and *S. plana* towards suspension feeding is a form of niche partitioning. Specialisation in particle size capture efficiency for a particular size range, as was expected for deposivores (Levinton, 1971) was not in evidence, for any Tellinoid species. Food selectivity of *L. balthica*, the deposivore, for larger plankton particles may be present in the field, as particles on *L. balthica*'s crystalline style were significantly larger than those on the other species. It is possible, however, that the plankton available on the sediment surface at the time *L. balthica* was feeding was significantly larger than those of the suspended seston. There was no narrow range of particle sizes on the style of *L. balthica*, which, together with the lack of a specific preferred particle size range in the clearance experiment suggests it may have been non-selectively feeding on larger particles available on the sediment. Such non-selective feeding by a deposivore would not be consistent with the predicted consequences of Levinton's (1971) hypothesis.

7.1 Future research

Future research in this field includes expanding the range of tests carried out and running SFG throughout the year. Collecting and analysing water and sediment samples and determining the size of food particle available would also help determine if spatial variation played a large role in the dietary results seen.

It would be of interest to perform experiments and investigations on specimens from areas where multiple species co-exist to see whether their physiology and energetics are influenced by the presence of competitors or the environment which supports those competitors. *S. plana*, *L. balthica* and *M. tenuis* are, for example, all found in Sandymount in Dublin Bay, while *M. tenuis*, *F. fabula* and *D. vittatus* (albeit in small numbers) are found at Blackrock. An extended study would differentiate not only between species, but between populations of each species, to establish whether feeding mode and physiological energetics vary within the populations of individual Tellinoid species of Dublin Bay. The expansion of this research to the sublittoral area of Dublin Bay would also allow a more comprehensive understanding of

Tellinoid dynamics in the entire bay.

7.2 Key findings and implications

The pattern of division of feeding modes between *S. plana* and *L. balthica* hasn't been observed previously. Both *L. balthica* and *S. plana* suspension- and deposit-feed depending on circumstances. The results of this investigation however, particularly the P:G and crystalline style plankton size distributions, suggest that *L. balthica* is a deposit feeder in Dublin Bay. The results for *S. plana* also suggest that, despite also deposit feeding to a certain extent, *S. plana*'s primary mode of feeding in Dublin Bay is suspension feeding. The ecological implications of such findings are that *L. balthica* should be classified as deposivorous and *S. plana* more suspensivorous in food web studies in Dublin Bay. Elsewhere, their modes of feeding may differ, however it is possible that this distinction emerges where the species occur sympatrically. A similar distinction can be seen between *M. tenuis* and *F. fabula*, suggesting an adaptation of one (*F. fabula*) to reduce potential competition. These have implications for energetic pathways through the ecosystem, and may result in a more efficient cycling of nutrients in the overall system, and a reduction in competitive effects of each species on the other.

It is clear that some of the species require certain conditions and food types, which may differ between geographic locations. Temporal and spatial quantification of functional groups, such as suspensivore and deposivore assemblages, is a more effective tool than presence of individual indicator species for assessing the impact of environmental disturbances (Putro *et al.*, 2014). It is important to have a precise classification of feeding mode of the species present in order to correctly characterise the functional groups. The results of this investigation will inform future estuarine ecosystem functioning analyses which can feed into environmental impact statements, as the feeding mode classification of *L. balthica* and *S. plana* will impact the ascribed importance of each functional group.

Another unexpected finding was that picoplankton <2μm dominated the plankton found on the crystalline style of *D. vittatus* which had been sampled from the field, and therefore had been consuming their natural diet. Picoplankton also constituted a substantial proportion of the natural diets of all Tellinoid species, except *L. balthica*.

The feeding modes, in Dublin Bay, of species which can suspension or deposit feed, were quantified more definitively, with *M. tenuis* being a suspension feeder, *L. balthica* a deposit feeder, and *S. plana* being a suspension/deposit feeder, with *S. plana* and *L. balthica*

more different than expected, potentially reducing potential competition between them. *M. tenuis* is the most successful Tellinoid overall in Dublin Bay, in terms of energetics, distribution and abundance. Not all of the predicted consequences of Levinton's (1971) hypothesis were observed to hold for the Dublin Bay littoral Tellinoidea, although predictions regarding community dominance in suspensivores and deposivores were supported. Feeding mode, physiological energetics and distribution of the littoral Tellinoidea in Dublin Bay were determined, providing insights into the functioning of the superfamily in terms of niche width and potential competition between species.

The littoral Tellinoids are an important component of the Dublin Bay ecosystem, (UNESCO Dublin Bay Biosphere) a site of high ecological value. A comprehensive understanding of the energy flows through Dublin Bay's ecosystems is vital for conservation purposes, and this work has contributed a greater understanding of the position and function of the Tellinoidea in Dublin Bay's food web.

The distribution and abundance of Tellinoidea in Dublin Bay revealed that most distributions were very similar to Wilson's (1982a) work, and showed little change in Dublin Bay's Littoral Tellinoidea in over 40 years. New methodological approaches were developed and refined to determine surface area of internal organs, and the palp to gill area ratio was successfully used to determine feeding mode, a result which allows a more defined feeding type to be used in feeding guild work. Using the crystalline style to determine diet was a new approach that was developed, and successfully showed differences in diet. The use of a coulter counter to determine suspended particle capture efficiency in terms of particle size in the littoral Tellinoidea of Dublin Bay was carried out for the first time, yielding clear differences among species, but not to the extent predicted as a consequence of Levinton's (1972) hypothesis. The understanding of Tellinoidean feeding, ecology and physiological energetics has been greatly expanded by this work.

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Appendix A

Palp:Gill Ratio

A.1 Comparison to existing measures of Palp/Gill Ratio

Compton *et al.*'s (2007) measurements of Gill:Palp mass ratios (Table A.1) are not comparable to the Palp:Gill Area ratios, but the relationship between gill area and gill mass is $Gill\ Area = k_g(Gill\ Mass)^{0.67}$, for some constant k_g, and the relationship between gill area and gill mass is $Palp\ Area = k_p(Palp\ Mass)^{0.67}$, for some constant k_p. Therefore, $Log(\frac{Palp\ Area}{Gill\ Area}) = k - 0.67 \cdot Log(\frac{Gill\ Mass}{Palp\ Mass})$ for $k = Log(\frac{k_g}{k_p})$, itself a constant.

Table A.1. Log(gill:palp mass ratios) from Compton *et al.* (2007)

$Log(\frac{Gill\ Mass}{Palp\ Mass})$	*M. tenuis*	*S. plana*	*L. balthica*
Lower Quartile	-0.1	-0.33	-0.36
Median	-0.05	-0.17	-0.3
Upper Quartile	0	-0.2	-0.25

Without knowledge of the precise value of k, comparisons may still be made between species examined by Compton *et al.* (2007), as the difference between any two species is unaffected by the value of k (Table A.2). The log of the differences between the median ratios of *M. tenuis* on the one hand and *S. plana* and *L. balthica* were 0.14 and 0.17 respectively, implying multiples of 1.37 and 1.48 respectively

Table A.2. Log(Palp:Gill Area Ratios) constructed by transforming Log(gill:palp mass ratios) from Compton *et al.* (2007) Note: absolute values are not provided due to unknown constant term, but differences are valid.

$Log(\frac{Palp\ Area}{Gill\ Area})$	*M. tenuis*	*S. plana*	*L. balthica*
Lower Quartile	0	0.13	0.17
Median	0.03	0.17	0.20
Upper Quartile	0.07	0.22	0.24

Appendix B

Data relating to Crystalline Style Analysis

B.1 Proportions of sizes and shapes in Tellinoid diets

B.2 Coefficients of ANOVA of Proportions against Size and Species

With *D. vittatus* and Shape B as the intercept or reference value

(Intercept)	speciesMB	speciesSP	speciesTF
0.64241000	-0.14278900	-0.21891200	-0.18643900
speciesTT	shapeB	shapeC	shapeD
-0.35280000	-0.63745100	-0.64232970	-0.64190600
shapeE	shapeF	shapeG	shapeH
-0.46261000	-0.63661000	-0.64241000	-0.64241000
shapeI	shapeJ	shapeK	shapeL
-0.63958000	-0.64241000	-0.59239000	-0.64241000
shapeM	shapeN	shapeO	shapeP
-0.64223900	-0.64241000	-0.64241000	-0.64241000
shapeQ	shapeS	shapeT	shapeU
-0.57407500	-0.63492000	-0.64230500	-0.60501000
shapeV	shapeW	shapeX	speciesMB:shapeB
-0.64241000	-0.64241000	-0.64241000	0.13783000

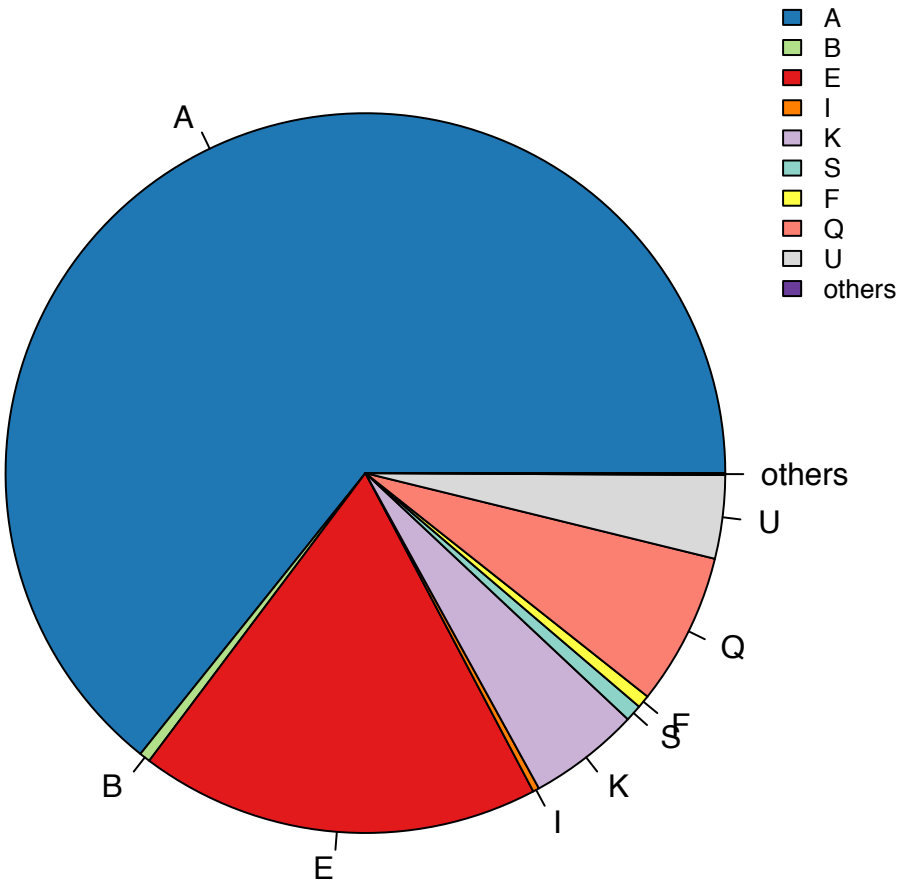

Figure B.1. Proportion of the total volume, of plankton by shape found on the crystalline style of *D. vittatus*. A description of the morphospecies can be found in Figure 4.5

```
speciesSP:shapeB speciesTF:shapeB speciesTT:shapeB speciesMB:shapeC
      0.21405500       0.18148000       0.41890100       0.19151185
speciesSP:shapeC speciesTF:shapeC speciesTT:shapeC speciesMB:shapeD
      0.37877680       0.20395270       0.36492340       0.14410500
speciesSP:shapeD speciesTF:shapeD speciesTT:shapeD speciesMB:shapeE
      0.35728000       0.19266550       0.44901600       0.26793000
speciesSP:shapeE speciesTF:shapeE speciesTT:shapeE speciesMB:shapeF
      0.22394700       0.45595900       0.55875400       0.17249900
speciesSP:shapeF speciesTF:shapeF speciesTT:shapeF speciesMB:shapeG
      0.21311200       0.22195200       0.35178000       0.14278900
speciesSP:shapeG speciesTF:shapeG speciesTT:shapeG speciesMB:shapeH
      0.22012200       0.20749900       0.35296800       0.14278900
```

```
speciesSP:shapeH speciesTF:shapeH speciesTT:shapeH speciesMB:shapeI
      0.21891200       0.18643900       0.36160400       0.13995900
speciesSP:shapeI speciesTF:shapeI speciesTT:shapeI speciesMB:shapeJ
      0.24772370       0.18594500       0.35000640       0.14278900
speciesSP:shapeJ speciesTF:shapeJ speciesTT:shapeJ speciesMB:shapeK
      0.21891200       0.18643900       0.44030000       0.09638224
speciesSP:shapeK speciesTF:shapeK speciesTT:shapeK speciesMB:shapeL
      0.21949900       0.13748440       0.33812000       0.14278900
speciesSP:shapeL speciesTF:shapeL speciesTT:shapeL speciesMB:shapeM
      0.21891200       0.18643900       0.36089000       0.14261800
speciesSP:shapeM speciesTF:shapeM speciesTT:shapeM speciesMB:shapeN
      0.21874100       0.18626800       0.35262900       0.14278900
speciesSP:shapeN speciesTF:shapeN speciesTT:shapeN speciesMB:shapeO
```

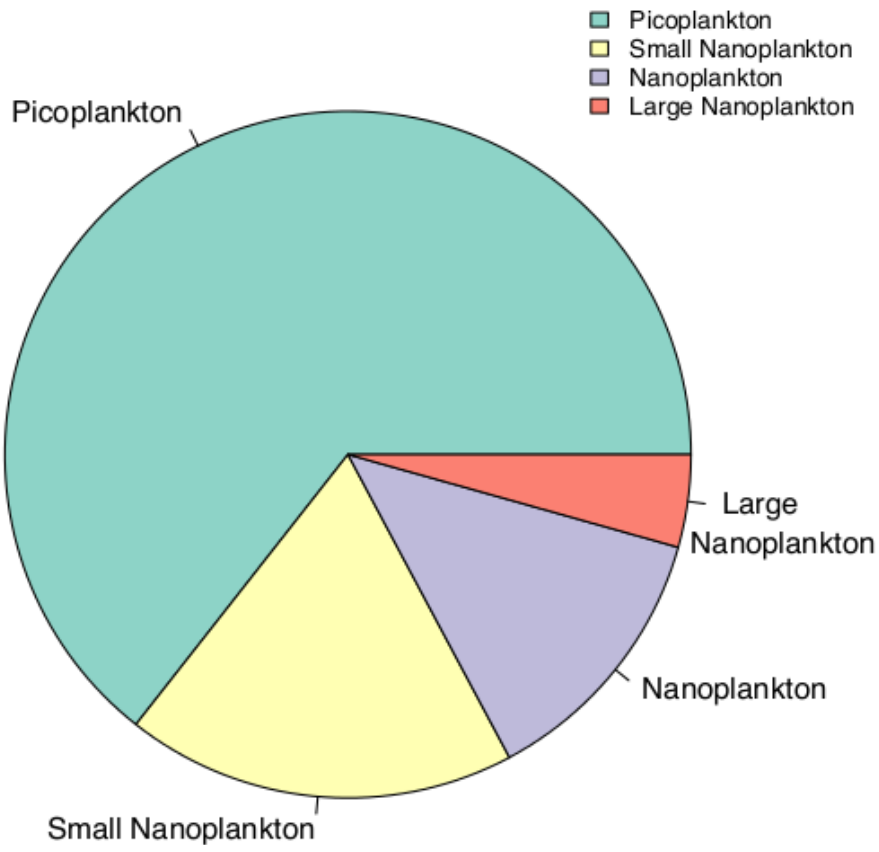

Figure B.2. Proportion of the total volume, of plankton sizes found on the crystalline style of *D. vittatus*. A description of the sizes can be found in Figure 4.1

Figure B.3. Proportion of the total volume, of plankton by shape found on the crystalline style of *M. tenuis*. A description of the morphospecies can be found in Figure 4.5

Figure B.4. Proportion of the total volume, of plankton sizes found on the crystalline style of *M. tenuis*. A description of the sizes can be found in Figure 4.1

Figure B.5. Proportion of the total volume, of plankton by shape found on the crystalline style of *F. fabula*. A description of the morphospecies can be found in Figure 4.5

```
      0.22400200       0.18643900       0.35280000       0.14640900
speciesSP:shapeO speciesTF:shapeO speciesTT:shapeO speciesMB:shapeP
      0.22220901       0.18643900       0.35280000       0.14278900
speciesSP:shapeP speciesTF:shapeP speciesTT:shapeP speciesMB:shapeQ
      0.21897380       0.18643900       0.35280000       0.17615370
speciesSP:shapeQ speciesTF:shapeQ speciesTT:shapeQ speciesMB:shapeS
      0.15057700       0.12248400       0.28446500       0.13529900
speciesSP:shapeS speciesTF:shapeS speciesTT:shapeS speciesMB:shapeT
      0.21188000       0.17894900       0.34531000       0.14268400
speciesSP:shapeT speciesTF:shapeT speciesTT:shapeT speciesMB:shapeU
      0.21908900       0.18633400       0.35269500       0.10538900
speciesSP:shapeU speciesTF:shapeU speciesTT:shapeU speciesMB:shapeV
      0.18151200       0.14903900       0.31540000       0.14314611
speciesSP:shapeV speciesTF:shapeV speciesTT:shapeV speciesMB:shapeW
      0.21891200       0.18643900       0.35280000       0.14278900
speciesSP:shapeW speciesTF:shapeW speciesTT:shapeW speciesMB:shapeX
      0.21891200       0.18643900       0.35280000       0.14294000
speciesSP:shapeX speciesTF:shapeX speciesTT:shapeX
      0.21891200       0.18643900       0.35280000
```

Figure B.6. Proportion of the total volume, of plankton sizes found on the crystalline style of *F. fabula*. A description of the sizes can be found in Figure 4.1

Figure B.7. Proportion of the total volume, of plankton sizes found on the crystalline style of *S. plana*. A description of the sizes can be found in Figure 4.5

B.3 Coefficients of ANOVA of Proportions against Size and Species

(Intercept)	sizem	sizen	sizepico
0.043570865	-0.043570865	0.084843155	0.600428603
sizesn	speciesMB	speciesSP	speciesTF
0.140444781	0.212759877	0.024448883	0.096477540
speciesTT	sizem:speciesMB	sizen:speciesMB	sizepico:speciesMB
0.048750628	-0.201638321	-0.007451057	-0.792231285
sizesn:speciesMB	sizem:speciesSP	sizen:speciesSP	sizepico:speciesSP
-0.062478721	-0.024448883	0.096840579	-0.268831563
sizesn:speciesSP	sizem:speciesTF	sizen:speciesTF	sizepico:speciesTF
0.074210648	-0.096477540	-0.224891560	-0.364877884
sizesn:speciesTF	sizem:speciesTT	sizen:speciesTT	sizepico:speciesTT
0.203859285	-0.048750628	0.067649149	-0.417640926

Figure B.8. Proportion of the total volume, of plankton sizes found on the crystalline style of *S. plana*. A description of the sizes can be found in Figure 4.1

Figure B.9. Proportion of the total volume, of plankton by shape found on the crystalline style of *L. balthica*. A description of the morphospecies can be found in Figure 4.5

Figure B.10. Proportion of the total volume, of plankton sizes found on the crystalline style of *L. balthica*. A description of the sizes can be found in Figure 4.1

```
sizesn:speciesTT
     0.154989267
```

Appendix C

Data Relating to Particle Size Experiment

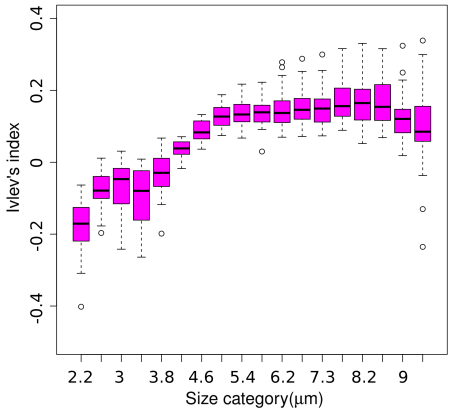

Figure C.1. Ranges of $\mathbb{E}$ by particle size category, *D. vittatus* . Black bars represent the median, magenta boxes the interquartile range, whiskers (lines extending vertically from the boxes) extend to the full range of the data lying not more than 1.5 times the interquartile range outside of the interquartile range ($n = 24$)

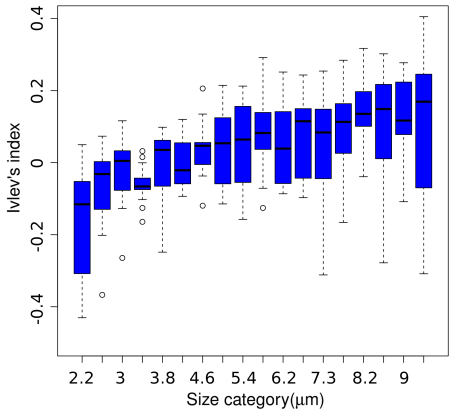

Figure C.2. Ranges of $\mathbb{E}$ by particle size category, *M. tenuis* . Black bars represent the median, blue boxes the interquartile range, whiskers (lines extending vertically from the boxes) extend to the full range of the data lying not more than 1.5 times the interquartile range outside of the interquartile range ($n = 16$)

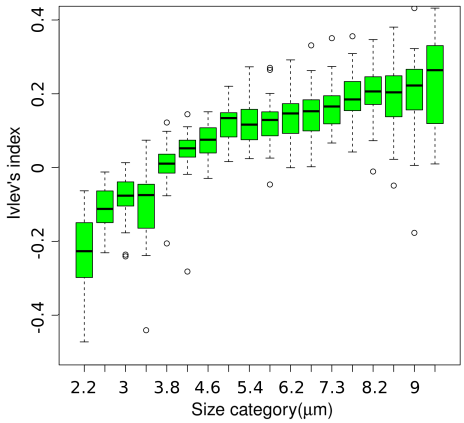

Figure C.3. Ranges of $\mathbb{E}$ by particle size category, *F. fabula* . Black bars represent the median, magenta boxes the interquartile range, whiskers (lines extending vertically from the boxes) extend to the full range of the data lying not more than 1.5 times the interquartile range outside of the interquartile range (n=28)

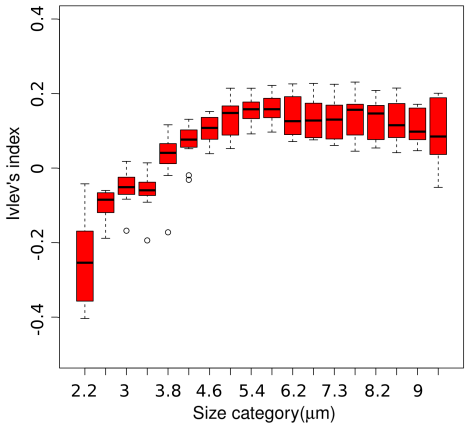

Figure C.4. Ranges of $\mathbb{E}$ by particle size category, *S. plana* . Black bars represent the median, red boxes the interquartile range, whiskers (lines extending vertically from the boxes) extend to the full range of the data lying not more than 1.5 times the interquartile range outside of the interquartile range ($n = 12$)

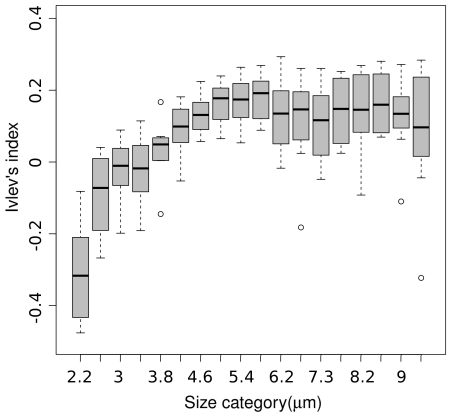

Figure C.5. Ranges of $\mathbb{E}$ by particle size category, *L. balthica* . Black bars represent the median, grey boxes the interquartile range, whiskers (lines extending vertically from the boxes) extend to the full range of the data lying not more than 1.5 times the interquartile range outside of the interquartile range ($n = 12$).